Carbon dynamics in restiad peatlands across different timescales

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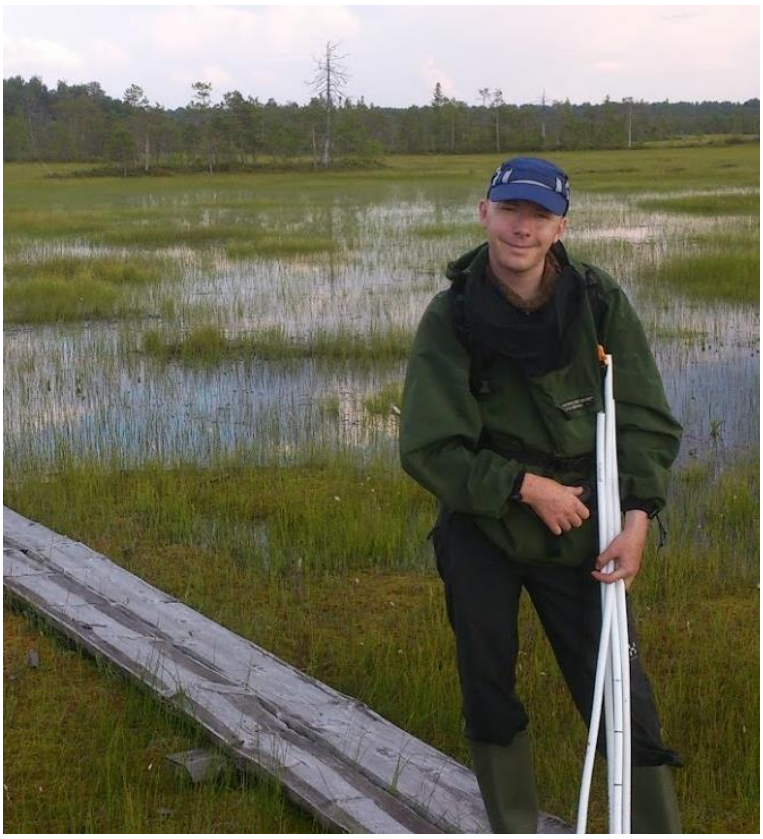

I would like to dedicate this thesis to my friend and former mentor; Dr. Richard Payne who died in an avalanche on the 26th of May 2019 while attempting to climb an un-named peak upon Nanda Devi mountain.

Abstract

Peatlands contain one of the largest terrestrial carbon stores on the planet, and one which is known to interact with climate and global biogeochemical cycling of nutrients. Peatlands maintain their carbon primarily through a high and stable water table which restricts decomposition, and large amounts of carbon can be lost upon drying. However, peatlands are also characterised by non-linear responses to external forcing with a complex array of internal feedbacks which tend to dominate ecosystem response over long-timescales and may amplify or dampen external influences. This has made predicting the effects of environmental change, beyond a few years, highly challenging. Here we use CO_2 fluxes and down-core measurements of carbon accumulation to study the drivers of peatland carbon exchange across a wide range of timescales. First of all, we compare contemporary CO_2 fluxes at two raised bogs, one of which is extremely dry in an international context (Moanatuatua), with the summer water table drawdown approaching one metre, and another where the water table is high and stable (Kopuatai). We found that despite the low and fluctuating water table in the impacted bog the site remained a sink for CO_2 which is strong in an international context, but reduced compared to the wet bog. A key factor in the wet bog being able to maintain a net sink for CO_2 was the enhanced photosynthetic capacity compared to the wetter bog, especially in summer, which was able to partially compensate for enhanced ecosystem respiration. There was a clear difference in how the two sites responded to contemporaneous water table drawdown, which was consistent with differences seen across wet and dry bogs in the international literature. We found plant productivity to be restricted at the dry bog, at both wet and dry extremes, while at the wet bog water table lowering stimulated ecosystem respiration, with neither effect being consistent across both bogs.

To further investigate how the dry bog, Moanatuatua, has adapted to low water tables we re-analysed CO_2 flux data from 1999 and 2000, a period at least several years after the water table initially dropped, and we compared this flux to the present day (after a 16 year gap). Re-analysis of the older data showed that in 1999 and 2000 Moanatuatua was a moderate source for CO_2 with elevated ecosystem respiration and lower photosynthetic capacity compared to the present

day. We attribute the change in photosynthetic capacity to the increased cover of the woody shrub *Epacris Pauciflora*, while a long term decline in ER would be consistent with changes in peat physical and chemical qualities as peat degrades making it further resistant to microbial decay.

In order to contextualise the CO_2 flux records and assess the drivers of carbon accumulation at the 50-100 year timescale we measured down-core C accumulation in unprecedented detail for a New Zealand bog, with supporting records available for fires, climate, eruptive events and plant species changes available from published and unpublished records at Moanatuatua. Contrary to our initial expectations, we found elevated C accumulation to be associated with at least three separate eruptive events, and possibly two others, with carbon accumulation rates increasing rapidly from a baseline typical of long-term accumulation rates, e.g. ~22 g C m^{-2} yr^{-1} to one which is more typical of contemporary uptake, 80-140 g C m^{-2} yr^{-1}. The complex eruptive history of the bog at this time makes it difficult to isolate any other effects, for instance climate. Geochemical analysis of the peat suggests increased phosphorus inputs as a mechanism for rapid C accumulation, with the peat stoichiometry recording a shift towards phosphorus abundance relative to carbon and nitrogen. The eruptive events linked to elevated carbon accumulation rates are also known to contain phosphorus within the volcanic glass and the mineral apatite, both of which would be expected to weather and become biologically available due both to processes within the eruptive plume and within the bog post-deposition. As such we have found the restiad bogs studied to be highly resilient to water-table drawdown in the long-term but in contrast, the C sink is highly sensitive to phosphorus inputs.

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I would like to acknowledge my chief supervisor David Campbell, for his friendship and excellent tutelage. Dave's students were always first priority for him and his technical expertise and attention to detail was exactly what I needed to develop my skills as a young scientist. In addition, Dave was always there for advice and support both professionally and personally. Louis Schipper kept me on track, taught me that less is more, that good science is not creating a baroque edifice, but rather that good Science is carried out incrementally, with precision and clarity. David Lowe was generous with his time and advice, displaying a enthusiasm and passion which was infectious; I especially appreciated his good-natured intelligence and subtle sense of humour, which was always present in my interactions with him. Beverly Clarkson lived up to her formidable reputation as a passionate and deeply knowledgeable peatland scientist. Many of the ideas in this thesis originated or were shaped by conversations with Bev and her enthusiasm and conviviality made her a joy to work with. Aaron Wall played an important role in the data analysis component of this thesis, and was always willing to offer help and advice, often combined with a humorous quip. Aaron had a leading role in designing and optimising many of the systems I used to process data. I found Aaron to be highly skilled and competent, I doubt it is possible to find a researcher who achieves a more perfect balance between attention to detail and efficiency and I hope to emulate his approach to data in my future work.

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take an interest in the natural world around them and she had a deep appreciation for knowledge in all forms, especially geology and history. She had a lifelong love of literature and was never far from a book. While working in the printing department of for Glaxosmithkline, she would return home with journal articles and technical reports, as they seemed interesting to her, and these were in due course passed on to me years later as a teenager. I have sought to emulate her independent mindedness, her stoic attitude to work, to poverty and to hardship. My mum has always valued education and her 'pushiness' and refusal to bow to entrenched class expectations was key in securing me a good education. She offered me a great deal of encouragement and guidance throughout my education. My dad spent years working in jobs he disliked to provide stability and an income for the family. His admiration for those that live an 'interesting' life, and scorn for petty corporate managers, was a further incentive for me to go into science. Doreen Worthington, my teacher when I was 6 years old, was exceptional, and further instilled in me a love of reading and of science. I still remember corresponding with Ms. Worthington sister, who at the time was excavating an ancient Egyptian tomb. Even the lowest achievers of our class all went on to get exceptional grades in science, and were also reasonably proficient in hieroglyphics. This was a real testament to her passion and abilities as a teacher. While studying for my A-levels at Barrow 6th form college Brian Gibson, my chemistry teacher, and at the time life coach, was another highly influential person for me. Brian was someone that clearly loved learning about a broad range of topics. He didn't just teach us, he cultivated our interest and made us want to learn.

I would like to thank the two anonymous reviewers who provided feedback and offered new perspectives upon the work contained in Chapter three, their input improved the final manuscript. I would like to acknowledge my former MSc examiner Richard Lindsay for his insights around peatland carbon cycling and his encyclopaedic knowledge of everything related to it. I really respect the way he thinks critically about the literature and hope I can emulate this in my own work.

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Chapter One

Introduction

1.1 The peatland carbon sink - threats and research questions

This thesis focuses on the drivers of peatland carbon cycling, specifically long-term changes associated with drying and nutrient enrichment. Improving understanding of long-term responses to drying has been repeatedly identified as one of the key questions facing peatland science (Dise, 2009; Limpens et al., 2008; Wieder et al., 2007). Additionally, nutrient cycling is tightly coupled to the peatland water table and is also independently being affected by human activity which may be more important for peatland carbon cycling than previously thought (Kylander et al., 2018).

Peatlands are a major component of the terrestrial carbon cycle with a proven role in past and present climate forcing, and a potential for large positive feedbacks to the climate system if the carbon stored within is lost (Limpens et al., 2008). Peatland carbon is immobilised primarily through a high and stable water table. Upon drainage, accompanied by conversion to intensive land use, peatlands lose a large amount of carbon (Evans et al., 2017) and CO_2 emissions from drained peatlands are projected to surpass the maximum theoretical mitigation potential of all agricultural soils (Leifeld and Menichetti, 2018).

Of considerable concern are the majority of peatlands which have not undergone drainage and land conversion, but may experience drying and destabilisation associated with climate change. Many peat-forming regions are experiencing climatically induced drying (van Bellen et al., 2018), others are predicted to dry in the future (Frolking et al., 2011; Shiogama et al., 2011) and there is a concern that the carbon contained within could be lost in response to this. Satellite measurements of humidity and near-surface water record water declines in major peat forming areas (Long et al., 2017; Zeng et al., 2014) while vast areas of peatland are undergoing vegetation changes as a result of drying or consistent with drying (Berg et al., 2009; McPartland et al., 2018).

Intact peatlands, however, are not fully analogous to peatlands drained for human use and considerable uncertainty exists as to how resilient they will be to drying

(Page and Baird, 2016; Spahni et al., 2013). Intact peatlands are complex ecosystems that possess the ability to self-regulate water-table and hydrology through a convoluted array of processes, the majority of which are tightly coupled to the carbon cycle. These processes have evolved over time to optimise water-use efficiency at the centennial to millennial timescale, rather than C accumulation as is sometimes assumed (Kettridge et al., 2015). Over 70 different interactions important for hydrological self-regulation have been identified by Waddington et al. (2015) and the relative strength, timing and sometimes even the direction of these interactions is only superficially understood. The effect of drying on carbon fluxes is equally complex. There is an apparent contradiction in how peatlands respond to drying across different timescales (Laiho, 2006), with a common pattern of high losses of C occurring initially (Alm et al., 1999; Laiho, 2006), followed by a recovery or even a strengthening of the C sink in the long-term (Laiho, 2006; Minkkinen and Laine, 1998). Somewhat paradoxically, dry[1] bogs can be insensitive to water table drawdown over the short term (one or two years), with no clear changes in vegetation or CO_2 fluxes (Lafleur et al., 2005), yet peatland theory suggests these bogs are the most vulnerable to future C loss (Belyea and Clymo, 2001; Hilbert et al., 2000), with dry sites being closer to the threshold of resilience beyond which the capacity of the ecosystem to self-regulate is overcome. There is a clear need to reconcile observations which, at least superficially, appear to be contradictory, and to provide data to test and develop theories and realistic models of peatland response to drying. One practical way in which this can be achieved is to study how CO_2 fluxes, and ecosystem function, differ with long-term water table position, and how they may change with time, in response to the internal processes and feedbacks triggered by water table lowering. Ecosystem function, in the context of gas and energy flux, can reasonably be viewed to encompass fundamental ecosystem processes such as photosynthesis, ecosystem respiration and water use.

[1] Dry bogs are defined here as having a mean annual water table depth of 400 mm or more from the peat surface. This is consistent with the way the term was applied in Lafleur et al. (2005)

1.2 Studying carbon dynamics in New Zealand peatlands

If theories developed from Northern Hemisphere peatlands are to be confidently applied to peatlands generally they need to be truly applicable across a range of different peat types (Bauer, 2004), thus we need to know how understudied peat types may respond to climate and disturbance (Limpens et al., 2008).

Peatlands in New Zealand are predominantly formed from vascular plants, of the family Restionaceae, and as such many New Zealand peatlands are referred to as 'restiad'. Restiad peatlands are interesting as they are climatically extreme, sitting outside of the zone where *Sphagnum* peatlands would normally be able to form raised bogs (McGlone, 2009), yet these extremely deep and organic rich peat deposits are not suggestive of marginal conditions for peat formation. Many of New Zealand's remaining lowland raised bogs are highly impacted by surrounding agriculture, with only small fragments left, and have historically been a poorly understood and poorly valued ecosystem type which is now at considerable risk of disappearing altogether, not least because their ecosystem functioning and resilience is so poorly understood. A greater understanding of the effect drying has had on restiad peatlands can thus meet two broad objectives:

1) Improved understanding of ecosystem function and resilience can inform conservation management of a threatened ecosystem.

2) Improved understanding of restiad bog dynamics is important for understanding ecosystem functioning in peatlands generally and will allow integration of New Zealand peatlands into global models and data compilations.

1.3 Moanatuatua and Kopuatai peatlands

Moanatuatua and Kopuatai peatlands are ideally suited to address the broad objectives of this thesis. Both are located within the Waikato region, which contains a greater area of mapped peatland than almost any other region in New Zealand, with the possible exception of Rēkohu, the Chatham islands (Ausseil et al., 2008) where the peat is extensive but is poorly mapped, although conservative estimates suggest more than 50,000 ha (Clarkson et al., 2004a; Macpherson and Hughson, 1943). Kopuatai is the only 'near-intact' example of the large *Empodisma robustum* raised bogs that once dominated the landscape (Irving et al., 1984), though a number of other small remnants exist throughout Waikato and Northland. Unlike the other peat types in New Zealand, the *E. robustum* bogs are

both better understood and easier to access than other restiad peatland types, *E. minus*[2] and *Sporadanthus traversii*[3].

Moanatuatua is an impacted peatland surrounded by dairy farmland. Once comparable in area to Kopuatai it is now reduced to a 140 ha remnant, less than 2% of the original extent (Clarkson et al., 2004b). The bog has undergone drying as a consequence of surrounding land-use change and was once formerly very wet with the water table at or near the surface, and it is now extremely dry in an international context with the water table approaching one metre deep in the late summer (Ratcliffe et al., 2019). Moanatuatua well-suited for studying the long-term effects of drying. Is almost certainly the best-studied peatland in New Zealand with at least 40 separate investigations being conducted since 1917 (S Table 1). Unusually for a peatland in New Zealand, descriptions, data and photographs exist from the period prior to the large changes wrought in the latter half of the 21st century and thus a baseline of 'pristine' conditions can be determined. A multi-year record of the peatland's CO_2 flux exits from the period shortly after the water-table decline is believed to have accelerated (circa 1996 in Clarkson et al., 1999) in 1999-2000 and a comparison with the present day would span an ecologically important time period seldom considered in the literature.

1.4 Thesis aims and objectives

The aim of this thesis is to better understand the drivers of peatland carbon flux across the 20-100 year timescale, specifically to capture the long-term changes the ecosystem undergoes as it adapts to change.

1) In order to study the effect of prior water table on peatland respond to environmental variables, we compare CO_2 fluxes and ecosystem function at Moanatuatua (drainage affected) and Kopuatai (near-pristine).

2) To study how the peatlands adapt to drier conditions and how this affects CO_2 exchange Moanatuatua bog will be re-visited after a 16-year interval in order to produce new CO_2 exchange measurements.

[2] Currently, only found south of 38° particualry common peatformer in high altitude bogs.
[3] Endemic to Rēkohu.

3) To investigate the dominant drivers of peatland carbon accumulation at 50-100 year time scales high-resolution record of C accumulation will be produced using a peat core.

1.5 Thesis Outline

The thesis is structured in the following way. Chapter 2 is a focused literature review designed to provide an up-to-date summary of the research which can inform the objectives and aims listed above, as well as identifying the gaps in understanding which provide motivation for the subsequent results chapters. Chapters 3-5 describe the main results of the research and specifically address each of the three thesis objectives listed above. Each of these chapters is treated as an independent manuscript with its own abstract, introduction, method and discussion. At the time of thesis completion Chapter 3 and Chapter 4, have been published by the journal *Science of the Total Environment* as Ratcliffe et al. (2019a; 2019b). Both have been included as chapters, without journal formatting. Chapter 5 has been submitted to the journal *Quaternary Science Reviews* but has not yet been peer reviewed. It is written in the same format as Chapters 3 and 4. As independent manuscripts, there is some inevitable repetition between Chapters 3-5. Chapter 6 summarises the overall results and conclusions obtained from this research and discusses the overarching themes that unify the main results chapters. The broader implications of the research and future research questions are also discussed.

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Chapter Two

Literature Review

2.1 Peatland as a carbon dense ecosystem

Peatlands store a vast amount of carbon, by most recent estimates 644 GT (Yu, 2011; Dargie et al., 2017). Unlike other terrestrial ecosystem systems, peatlands can accumulate carbon almost indefinitely (Belyea and Baird, 2006; Treat et al., 2019). Despite occupying only 3% of global land area (Yu et al., 2010), the peatland carbon store is geological in magnitude, equivalent to more than all the fossil fuels burnt from 1870 till 2018 (435 GT C in: Le Quéré et al., 2018). Unlike geological carbon stores, peatland carbon is stored close to the atmosphere, within a living ecosystem, which interacts with the global climate system (Yu et al., 2011). As such peatlands are responsive to external perturbations. The peatland carbon store is prevented from oxidising primarily due to a high and stable water table which slows oxygen diffusion and creates an environment unfavourable for oxidative carbon loss. Typically the loss of a high and stable water table through either change in climate, or anthropogenic drainage, results in the loss of some or all this carbon (Armentano and Menges, 1986). Currently, artificially drained peatlands are thought to be losing 0.55 GT C per year (Joosten, 2009), which in context is equivalent to about 6 % of global fossil fuel emissions (9.4 GT C yr^{-1} in Le Quéré et al., 2018). These emissions originate from an estimated 11.2 % of peatland area which has been drained (Joosten, 2009). Of considerable concern are the large areas of undrained peatland which are likely to experience drying due to climate change (Frolking et al., 2011). It is uncertain whether these peatlands will act as a positive or negative feedback in response to predicted drying (Yu et al., 2011), i.e. will they continue to sequester carbon as they have done in the past, or could they release the carbon stored in the form of CO_2.

2.2 Peatland response to drying predicted and observed

Many natural peatlands around the world are undergoing climatically driven drying (Frankl and Schmeidl, 2000; Oechel et al., 2000; Hendon and Charman, 2004). Changes in vegetation, consistent with drying, are also occurring on a large scale. For instance, there has been an expansion of woody shrubs across peatlands in North America and Europe (Frankl and Schmeidl, 2000; Malmer and Wallén,

2004; Klein et al., 2005; Chambers et al., 2007b; Berg et al., 2009; Kapfer et al., 2011; Hedwall et al., 2017; McPartland et al., 2018). In parts of Canada and Siberia tree cover is expanding onto open bogs (Pellerin and Lavoie, 2003; Linderholm and Leine, 2006; Blanchet et al., 2017; Ratcliffe et al., 2017). Some of these changes are on a scale hitherto unprecedented in the peatland landscape (Chambers et al., 2007a; Berg et al., 2009; Ratcliffe et al., 2017). Further expansion of trees and shrubs is expected, due to a combination of increased drought and warmer temperatures (Heijmans et al., 2013; Radu and Duval, 2018). Currently, there is very little known about how the changes that have been seen, and are predicted to occur, in drying peatlands will impact on the peatland carbon balance in the long-term. For instance, it has been proposed that shrub expansion may be a long-term self-adaptive mechanism increasing carbon sequestration and protecting historic carbon stocks (H. Wang et al., 2015), while a contradicting view is held that shrub expansion may destabilise the peatland carbon store (Walker et al., 2016). Others speculate that shrub expansion is simply a transitional stage in vegetation change, which will facilitate tree encroachment (Holmgren et al., 2015), the results of which are largely unknown in terms of carbon fluxes, as was noted by Ratcliffe et al., (2017).

2.3 Peatlands as complex non-linear systems

Much of the uncertainty of how peatland carbon will respond to future climate stems from the complex internal responses a peatland undergoes which may dampen or amplify the response induced by external drivers (Laiho, 2006; Waddington et al., 2015). Peatlands should be viewed as complex adaptive systems, in that they display spatial heterogeneity, a self-organising structure and non-linear responses to external forcing (Belyea and Baird, 2006). It is common for peatlands to display long periods of little change, punctuated by abrupt transitions of state (Hilbert et al., 2000; Eppinga et al., 2007), even under weak or steady environmental forcing, and they may respond to external forcing at unexpected frequencies (Hilbert et al., 2000; Belyea, 2009). Because of this there is considerable debate as to the stability of the peatland carbon sink, with some studies suggesting peatlands will continue to sequester carbon in the coming century (Wilson et al., 2016; Gallego-sala et al., 2018), others cautioning that peatlands may respond to predicted changes in climate with large losses of C. (Bridgham et al., 2008; Ise et al., 2008) and others state that either scenario could

occur, depending on the degree of 21st century warming (Spahni et al., 2013). Importantly, we have almost certainly not yet identified all of the important feedbacks that affect peatland behaviour (Page and Baird, 2016). Current modelling approaches work from the assumption that known relationships between carbon and climate, determined from very different timescales, will correctly predict carbon dynamics over the time-period of interest. For example Ise et al., (2008) used contemporary relationships between water balance, water table and ecosystem respiration to extrapolate the effect of lowered water balance from decades to thousands of years into the future, failing to incorporate important long-term processes such as changes in peat hydrological properties (Page and Baird, 2016) which can be a major mechanism of peatland resilience to drying operating at the decadal to centennial timescale (Waddington et al., 2015). More recently, Gallego-sala et al., (2018) coupled the carbon accumulated over a 1000 year period, with contemporary climatic variables, to predict how peatlands will respond to climatic change over 20-year timescales. This is problematic for a number of reasons. In short Gallego-sala et al., (2018) took the net result of processes, some of which we know to take place over a century or more (Swindles et al., 2012; Kettridge et al., 2015), and applied these to a much shorter time period. Additionally, carbon accumulation rates measured over the past 1000 years are also often in contrast to contemporary C uptake (Ratcliffe et al., 2018a) and this is clearly something which needs to be addressed if long-term C accumulation rates are to be used to predict C dynamics in the near future. Therefore, current modelling approaches have been less than ideal, and there is as yet no consensus as to what will happen to the peatland carbon store over the coming century (Frolking and Roulet, 2009; Page and Baird, 2016). As stated by Dise (2009), unless the strong feedbacks inherent in peatlands are considered there is a risk that their response to global change will be substantially under- or over-estimated. To build upon this statement, it is also necessary to consider drivers and feedbacks that are relevant for the time period of interest.

2.4 Terminology related to carbon cycling across timescales

In order to investigate carbon cycling in peatlands, it is necessary to consider the components of the ecosystem carbon balance and to what degree they are captured by different measurement techniques across different timescales. The terminology for peatland carbon cycling can be somewhat complex and it is not to be taken for

granted that the majority of investigators will be familiar with all terms, as a considerable number of terms and acronyms exist for both long-term and contemporary carbon cycling, with much cross-over and duplication within the literature. These terms and acronyms are summarised visually in the figure below (Fig 2.1) and are also described in Table 2.1. While we use some of these terms in this thesis, others are superfluous or have duplicate meanings. We have distinguished the terms used in this thesis in bold to differentiate them. This author agrees with the assertion that the purpose of acronyms should be to speed up reading and ease the understanding of content (Mack, 2017). Acronyms, used to excess, do not serve this purpose and instead serve only to obscure meaning. We, therefore, seek to use acronyms sparingly, preferring to avoid them altogether in sections of the thesis where work is summarised, and avoiding unconventional or unfamiliar acronyms whenever possible.

Table 2.1: Acronyms and terms used in peatland carbon cycling with examples of definitions from the literature

Acronym	Full name	Description	Example reference(s)
NEE	Net ecosystem exchange	CO_2 exchange between the ecosystem and the atmosphere. The negative sign indicates ecosystem uptake	(Chapin et al., 2006)
GPP	Gross primary production	Ecosystem plant productivity also NEE-ER	(Chapin et al., 2006)
ER	Ecosystem respiration	Sum of all respiration processes, including autotrophic and heterotrophic	(Chapin et al., 2006)
NPP	Net primary production	Analogous to the production of organic matter by plants GPP-autotrophic respiration	(Chapin et al., 2006)
SR/R_{het}	Soil respiration/hetrotrophic respiration	Microbial respiration	(Chapin et al., 2006)
NEP	Net ecosystem production	Opposite sign convention to NEE, more commonly used for summed values	(Chapin et al., 2006)
AD	Abiotic degradation	The pathway where organic compounds are broken down by abiotic processes	(Rutledge et al., 2010)
FCH_4	Flux methane	Microbially respired CO_2 from the breakdown of CH_4	(Nielsen et al., 2019)
CAR	Carbon accumulation rate	Carbon accumulation in catotelm peat covering any period	(van Bellen et al., 2011)
LORCA/LARCA/FLARCA	The long-term apparent rate of carbon accumulation,	Carbon accumulation rate spanning an entire peat core	(Tolonen and Turunen, 1996; Lindsay, 2010)
ARDA/P*	The actual rate of deposition by the acrotelm	The rate of organic matter moving from the oxic acrotelm into the relatively stable anoxic catotelm	(Clymo, 1978; Lindsay, 2010)
ARCA/TRACA	The actual/true rate of carbon accumulation	The rate of input into the catotelm minus the loss of carbon from the entire system, difficult to measure in	(Tolonen and Turunen, 1996)

Acronym	Full name	Description	Example reference(s)
		practice.	
RERCA/NFRCA	The recent rate of carbon accumulation	Rate of carbon accumulation in the surface peat. Typically only spans part of the last 100 years	(Billett et al., 2010)
DOC	Dissolved organic carbon	Organic carbon lost in dissolution via peat water	(Rydin et al., 2006)
DIC	Dissolved inorganic carbon	Respired carbon lost in peat water	(Rydin et al., 2006)
POC	Particulate organic carbon	Carbon lost through wind, or aquatic carbon exports. Significant for eroding peatlands and could include pollen from restiad peatlands	(Rydin et al., 2006)
CH4	Methane	Carbon-containing greenhouse gas produced in anoxic conditions by peatland microbes	(Rydin et al., 2006)
BVOC	Biological volatile organic carbon	Typically trace amounts of organic compounds which are volatilised, examples include compounds involved in plant hormonal signalling	(Faubert et al., 2010)

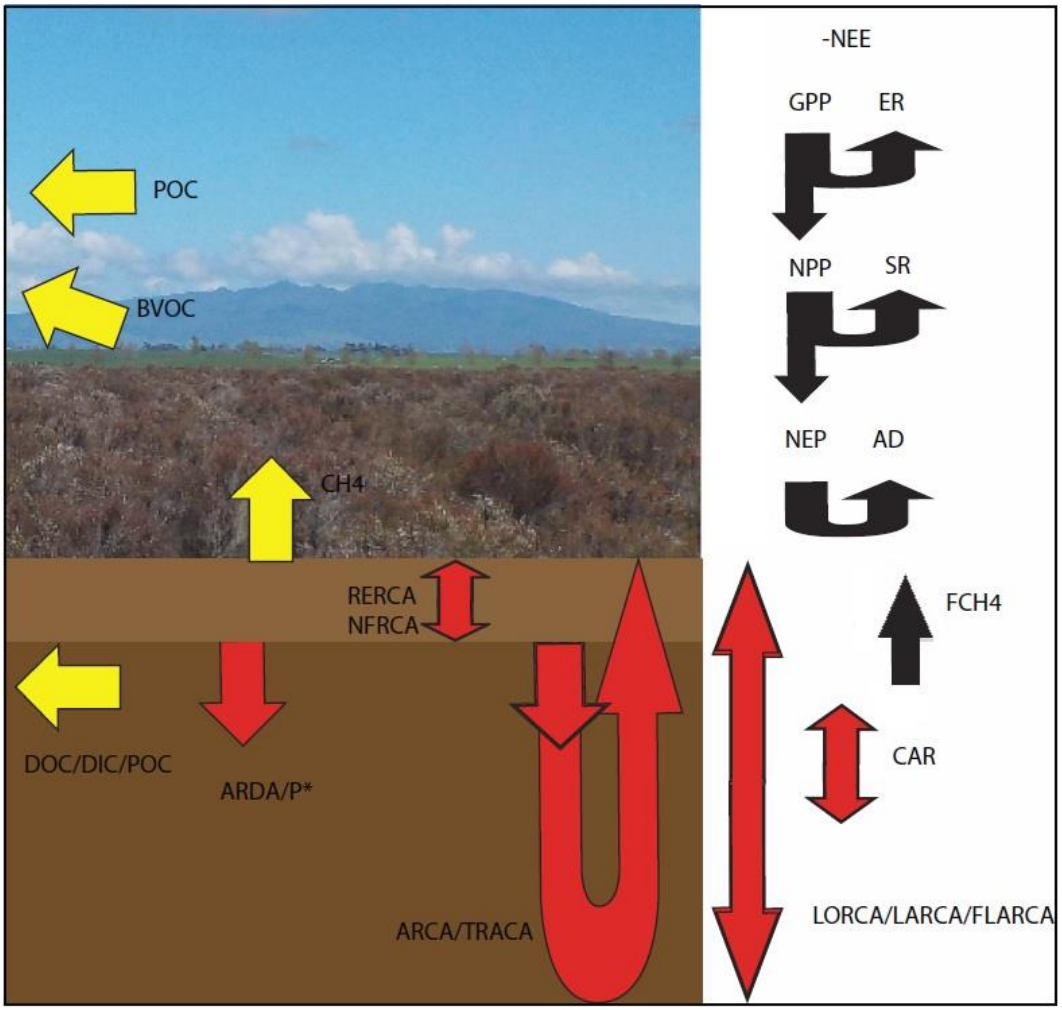

Figure 2.1: Diagram summarising the terms used in describing peatland carbon flux. Terms used in this thesis are highlighted in bold. The processes are colour coded with black pertaining to CO_2 flux terminology, red represents long-term carbon cycling terminology and yellow represents non-CO_2 components of the peatland carbon balance.

It should be noted that many contemporary studies of C exchange focus on the CO_2 flux components only, due to the considerable extra time and money that is required to measure other components of the carbon balance. Even in studies which purport to be presenting a net ecosystem carbon balance (NECB), which are the minority of peatland CO_2 flux studies, the quality of non-CO_2 measurements is often much lower, and typically only DOC and CH_4 are considered. For instance, the DOC export at Forsinard, Scotland was calculated for the entire catchment, from a river outflow 10km from the site (Levy and Gray, 2015) and included run-off from both mineral soil and afforested peatland, in addition to the "semi-natural peatland" eddy covariance footprint (Ratcliffe, 2015). All peat core measurements are inclusive of the entire C balance, while only a

small minority of flux sites report the total C balance, thus the scarcity of reliable full carbon balance complicates comparisons across timescales. However, depending on the context, it can still be entirely appropriate to make comparisons between CO_2 flux only and below ground C stocks, allowing for realistic estimates of non-CO_2 losses. The reason for this is that non-CO_2 carbon fluxes tend to be small in comparison to that of CO_2, and tend to sit within a more tightly confined range of values. Very wet peatlands, such as fens, may have high CH_4 (e.g. 35 g C yr^{-1} in Bäckstrand et al., 2010) but would be expected to have low DOC exports, whereas dry bogs and drained bogs may be expected to have very low CH_4 but potentially 'high' DOC (Strack et al., 2008; Dinsmore et al., 2010). Taken altogether, non-CO_2 exports of carbon are unlikely to exceed 50 g for temperate peatlands and literature measurements would suggest they are much lower than this. For instance, the combined CH4 and DOC loss from Kopuatai bog is 29 g C m^{-2} yr^{-1} (Goodrich et al., 2017) compared to <15 g C m^{-2} yr^{-1} for two intact bogs where NECB is reported (Gažovič et al., 2013; Levy and Gray, 2015) and in all these three examples the non-CO_2 flux was <20% of the NECB. For other sites which are impacted by drainage and grazing, such as Auchencoerth in Scotland, the total non-CO_2 flux contribution is, depending on your perspective, more significant for the C balance due to the lower net CO_2 uptake (Dinsmore et al., 2010). However, it could also be argued that the non-CO_2 loss remains minor as it is smaller (31 g C m^{-2} yr^{-1} in Dinsmore et al., 2010) than the realistic uncertainty associated with CO_2 flux calculation (50 g C m^{-2} in Baldocchi, 2003).

2.5 Measuring peatland C across timescales, introduction

Eddy covariance (EC) is considered one of the best techniques for investigating ecosystem-scale carbon fluxes (Aubinet et al., 2012) but until recently running multiple sites was rare, due to expense, and producing long datasets was technically challenging. Applied in the traditional sense, i.e. multiple years of EC measurements from a single site, a snapshot of the CO_2 balance is presented. This is informative of how the ecosystem functions in the present, but is typically too short to capture the slow, low frequency, changes which appear to dominate the way peatlands interact with climate over longer, i.e. decadal to centennial timescales (Mäkiranta et al., 2009; Straková et al., 2012). Key peatland feedbacks may take decades or longer to take effect (Swindles et al., 2012; Kettridge et al., 2015) and this is simply not a practical timespan for carrying out continuous

measurements. Ecosystem functioning can be compared over longer timescales in drying peatlands by using space for time substitution, (e.g. Chimner et al., 2016; Hargreaves et al., 2003), by re-visiting earlier measurements carried out in drying peatlands (Chapter Four, this thesis), or by making use of palaeoecological techniques (Mauquoy et al., 2002; Yu, 2011; Ratcliffe et al., 2018a). Each approach has strengths and weaknesses, and a combination of all three offers a powerful way to assess the effect of drying across timescales.

2.6 The short term response of peatlands to water table movement.

Generally speaking, contemporary flux literature has tended to consider peatlands as static systems, responding to environmental drivers in a contemporaneous and consistent manner. There are some important exceptions to this. In some of the longer datasets, it has become possible to explore non-contemporaneous relationships between climatic drivers and CO_2 flux. This has been done by Helfter et al., (2015) and Peichl et al., (2014) who found that winter temperatures offered the best determinant of summer GPP, independent of growing season length. While the exact mechanism behind this is unknown, it is suspected to be nutrient-mediated (Peichl et al., 2014). The fact that such a relationship can be the dominant driver of CO_2 flux in longer eddy covariance records demonstrates that non-linear processes can drive CO_2 exchange even on an interannual basis and are an important aspect of the peatland carbon-cycle.

Table 2.2: A compilation of published EC records and the relationship found between the water table and ecosystem CO_2 fluxes. The mean water table and the upper and lower range are provided when available. The sites are divided into 'dry' sites when the mean water table depth (WTD) is below 200 mm and 'wet' sites where the mean WTD is above 200 mm. An additional category is provided for sites and compilations where the water table was not clear.

Dry sites									
Site name	Peat type	Dominant species & Family in parenthesis	Mean WTD (mm)	Shallowest WTD (mm)	Deepest WTD (mm)	NEP	ER	GPP	Reference
Mooseurach	Drained, forested	*Picea abies* (Pinaceae)	-220	- 50	-450	No relationship	No relationship	Not reported	(Hommeltenberg et al., 2014)
Moanatuatua	Drained bog	*Empodisma robustum* (Restionaceae)	-580	-327	-813	No relationship	No relationship	Not reported	(Campbell et al., 2014)
Mer Bleue	Intact bog	*Chamaedaphne calyculata* (Ericaceae)	-400	-300	-650	Decrease	No relationship	Decrease	(Dimitrov et al., 2011)
Mer Bleue	Intact bog	*Chamaedaphne calyculata* (Ericaceae)	-450	-200	-750	No relationship	No relationship	Not reported	(Lafleur et al., 2005)
Lost Creek	Treed fen	*Alnus incana* (Betulaceae) *Carex* spp. (Cyperaceae)	-250	+380	-820	No relationship	increased	increased	(Sulman et al., 2009)
Monte Bondone	Poor fen (disturbed ?) **	*Molinia caerula* (Poaceae) *Carex rostrate* (Cyperaceae)	-270	-20	-600	decreased	increased	decreased	(Pullens et al., 2016)
Western Peatland	Treed rich fen	*Picea mariana* (Pinaceae) *Betula pumila* (Betulaceae)	-480 (est)	-280	-620	No relationship	increased	increased	(Flanagan and Syed, 2011)
SNWR - Dry	Poor fen	*Chamaedaphne calyculata* (Ericaceae) Carex spp. (Cyperaceae)	-368	-200	-500	decrease	Not reported	Not reported	(Chimner et al., 2016)

Site name	Peat type	Dominant species & Family in parenthesis	Mean WTD (mm)	Shallowest WTD (mm)	Deepest WTD (mm)	NEP	ER	GPP	Reference
SNWR - Ref	Poor fen	*Sphagnum* angustifolium *Chamaedaphne calyculata* (Ericaceae)	-216	-180	-420	decrease	Not reported	Not reported	(Chimner et al., 2016)
Kalevansuo	Drained bog	*Pinus sylvestris* (Pinaceae) *Vaccinium myrtillus* (Ericaceae)	-500 (est)	-300	-800	No relationship	Not reported	Not reported	(Minkkinen et al., 2018)
Palangkaraya	Drained tropical peatland	*Combretocarpus rotundatus* (Anisophylleaceae) *Cratoxylum arborescens (Hypericaceae)*	-700 (est)	-200	-1750	No relationship	Parabolic	Not reported	(Hirano et al., 2007)
Yenicaga	Rich fen	*Phragmites australis* (Poaceae) *Typha domingensis* (Typhaceae)	-400 (est)	0	-800	decreased	increased	increased	(Aslan-Sungur et al., 2016)
Wet sites									
Kopuatai	Intact bog	*Empodisma robustum* (Restionaceae)	-120 (est)	+ 5	-250	decreased	increased	No relationship	(Goodrich et al., 2015)
Bourtanger Moor	Moderate drainage,	*Erica tetralix* (Ericaceae) *Molinia caerulea* (Poaceae)	-100	20	-550	Decrease	increase	Not reported	(Hurkuck et al., 2016)
Western Canada	Intact fen, treed	*Larix laricina* (Pinaceae) *Andromeda Polifolia* (Ericaceae)	+100 (est)	+400	-400	Parabolic	- Not reported	Parabolic	(Sonnentag et al., 2010)

Auchencorth	disturbed bog	*Deschampsia flexuosa* (Poaceae) *Sphagnum papillosum* (Sphagnaceae)	-35	+50	-380		Parabolic	decreased	(Helfter et al., 2015)
Lompolojänkkä	Intact fen	*Betula nana* (Betulaceae) *Menyanthes trifoliate* (Menyanthaceae)	+20 (est)	+60	-20	decreased	- Not reported	decreased	(Aurela et al., 2009)
Siikaneva	Poor fen	*Eriophorum vaginatum* (Cyperaceae) *Carex rostrate* (Cyperaceae)	-50 (est)	+40	-280	parabolic	Parabolic	- Not reported	(Aurela et al., 2007)
Fajemyr	Intact bog	*Calluna vulgaris* (Ericaceae) *Erica tetralix* (Ericaceae)	-39	+40	-250	decreased	increased	decreased	(Lund et al., 2012)
Salmisuo	Intact treed fen	*Sphagnum papillosum* (Sphagnaceae) *Sphagnum fuscum* (Sphagnaceae)	-100 (est)	-50	-280	decreased	increased	No relationship	(Gažovič et al., 2013)
Forsinard	Intact blanket bog	*Sphagnum* spp. (Sphagnaceae) *Eriophorum* spp. (Cyperaceae)	-80 (est)	0	-400	No relationship	- Not reported	- Not reported	(Levy and Gray, 2015)
Lac Le Caron	Intact bog	*Sphagnum fuscum* (*Sphagnaceae)* *Kalmia angustifolia* – (Ericaceae)	-80 (est)	+50	-290	decreased	increased	decreased	(Strachan et al., 2016)
Glencar	Disturbed blanket bog	*Molinia caerulea*, (Poaceae) *Calluna vulgaris*, (Ericaceae)	-48	0	-150	decreased	increased	decreased	(McVeigh et al., 2014)
Degerö Stormyr	Poor fen	*Eriophorum vaginatum* (Cyperaceae) *Trichophorum*	-180 (est)	20	-400	parabolic	parabolic	parabolic	(Peichl et al., 2014)

		cespitosum (Cyperaceae)							
SNWR - Wet	Poor fen	*Chamaedaphne calyculata*, (Ericaceae) *Sphagnum angustifolium* (Sphagnaceae)	-121	+50	-250	Parabolic?	Not reported	Not reported	(Chimner et al., 2016)
Tanana Flats a)	Scar bog	*Sphagnum riparium* (Sphagnaceae)	-100 (est)	+80	-250	decreased	decreased	decreased	(Euskirchen et al., 2014)
Tanana Flats b)	Rich fen	*Drepanocladus* spp. (Amblystegiaceae) *Sphagnum* spp. (Sphagnaceae)	0 (est)	+450	-380	decreased	Parabolic	Parabolic	(Euskirchen et al., 2014)
Sites for which the water table is not described									
Kaamanen	Intact fen	*Ledum palustre* – (Ericaceae) *Carex* spp. (Cyperaceae)	N/A	N/A	N/A	Mixed*	- Not reported	- Not reported	(Aurela et al., 2004)
Andøya	Blanket bog (disturbed ?)	N/A	N/A	N/A	N/A	No relationship	No relationship	No relationship	(Lund et al., 2015)
Multiple sites	N/A	N/A	N/A	N/A	N/A	decreased	increased	decreased	(Lund et al., 2010)

With regards to the water table, a diverse range of contemporaneous responses have been recorded for peatland CO_2 fluxes in response to water table drawdown, offering almost every conceivable relationship, including positive, negative, parabolic and no relationship (Table 2.2), visualised in figure 2.2.

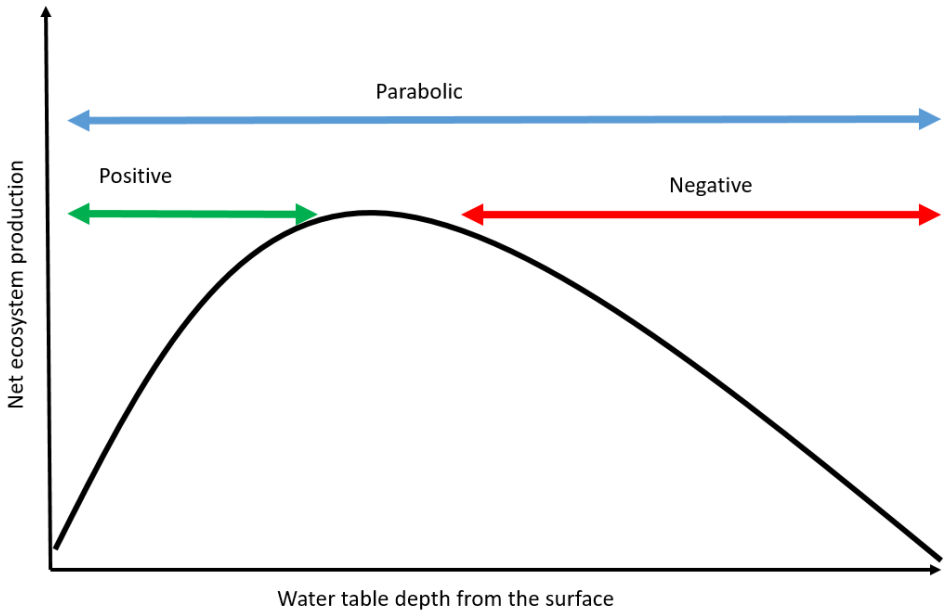

Figure 2.2: Conceptual diagram of peatland response to water table changes, showing negative, positive and parabolic relationships between primary productivity and water table depth.

While the lack of consistency between sites is sometimes noted (e.g. Sulman et al., 2010), a general explanation for the lack of consistency has not been proposed. There are existing theoretical frameworks that offer a good explanation for such variation, and these have been developed with the consideration that peatlands are non-static, non-linear systems. One such framework is that of (Belyea and Clymo, 2001).

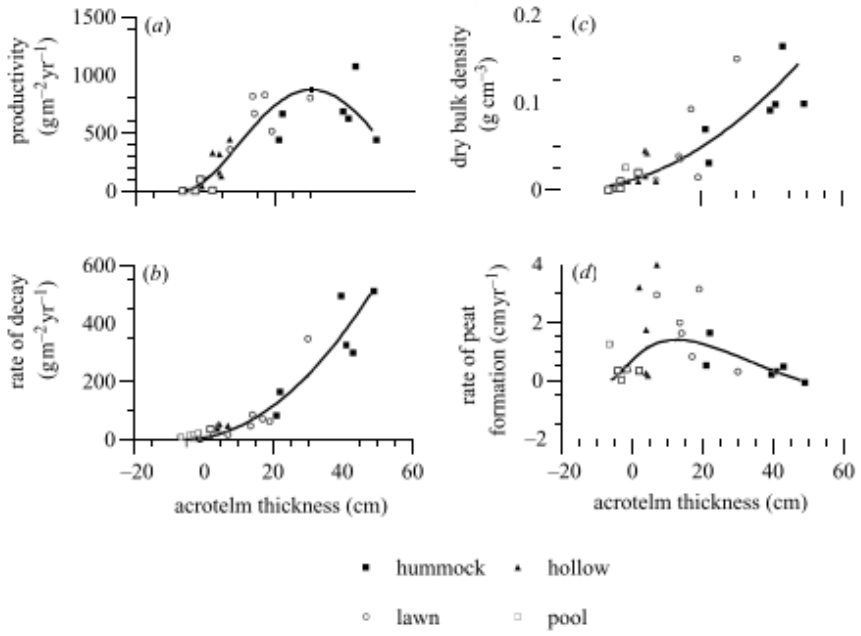

Figure 2.3: Taken from Belyea and Clymo 2001. Data is for Ellergower Moss, UK a) shows plant productivity as assessed by the mass balance method, b) the cumulative decay in the acrotelm, C) the dry bulk density d) the rate of peat formation. The curves in a-c are polynomial regressions and d) is an arithmetic combination of the regressions in a-c.

Some of the main ideas outlined by Belyea and Clymo are a) that prior water table is important for the response of carbon to water table b) that a change in water table will induce a greater response in a wet peatland than a dry one, unless a threshold of stability is crossed and c) internal feedbacks tend to maintain a stable shallow water table depth, unless the water table depth passes beyond a certain threshold.

The ideas proposed by Belyea and Clymo (2001) provide a useful way of understanding the different responses seen in the flux literature. For instance, when in wet peatlands the peatland water table is high, NEP is almost always found to have a relationship with WTD (12 out of 13 wet sites in Table 2.2), while for dry peatlands a majority (7 out of 11 dry sites in Table 2.2) found no relationship between water table and NEP. This is not to say that such a relationship does not exist in dry peatlands, it would be expected to exist (Belyea and Clymo, 2001), and clearly does for number of sites, but rather it is likely to be weaker than for a wet peatland and therefore less likely to be detected, particularly if variation in water table is not exceptionally high for the site. This was determined to be the case in Lafleur et al. (2005) who explained the lack of

relationship between CO_2 losses through ER and water table at a typically dry Canadian bog. By using laboratory incubations, they found that both the surface peat (0-5cm) and the deep peat (40-45 cm) were in fact responsive to changes in moisture content, with moisture content having very little effect on CO_2 production at other depths. As typical water table fluctuations did not affect the moisture content of the surface or the deep peats, the water table fluctuation measured did not have an effect on CO_2 fluxes (Lafleur et al., 2005).

While the framework of Belyea and Clymo (2001) is useful for interpreting the range of responses seen in Table 1 it was developed using data from a limited number of peatland species, mostly *Sphagnum* mosses, and a limited range of water table variability. The various thresholds outlined, (i.e. the optimal water table depth for peat production) can be expected to be quite different, depending on the vegetation of the peatland. There is good evidence to support the idea of a parabolic relationship (Figure 2.2) between net ecosystem productivity and water table which is often seen when the range of water table fluctuation is sufficiently large (e.g. 800 mm in Sonnentag et al., 2010).

It is also now known that the relationship between decay and water table depth is considerably more complex than that described in Belyea and Clymo (2001) and it often has a primary as well as a secondary optima, with the first optima indicating the oxygenation of the labile carbon-rich surface peat, and the second the oxygenation of the normally anoxic catotelm peat below the usual range of water table fluctuation (Laiho, 2006). Respiration can even decline with a falling water table at very low water table depths as microbial activity within the surface peat becomes moisture limited (Urbanová and Bárta, 2016). The framework is, in essence, a useful way to interpret contemporary relationships between the water table and carbon in peatlands, but is constrained by the limited dataset used to construct it. While it appears to work well for *Sphagnum*-dominated bogs, the thresholds and optima can be expected to be quite different for peatlands with predominantly vascular vegetation, as would be the case for most modified bogs.

2.7 Long term response to water table movement

When long-term water table position is considered as a regulator of peatland CO_2 flux the role of contemporary water table variation becomes much clearer. While high-frequency (sub-annual) forcing can be quite weak, low-frequency forcing

(decadal) is usually strong (Mäkiranta et al., 2009; Straková et al., 2012; Frolking et al., 2014) acting upon the vegetation community in ways which may change fundamental photosynthetic properties and the quality of litter available for microbial breakdown.

2.7.1 Eddy Covariance measurements of CO_2 flux following long term water table lowering

Measuring the effect of long-term water table change in peatlands is challenging. Natural drying is difficult to detect in intact peatlands, for instance, historical water table measurements would have been available (e.g. Frankl and Schmeidl, 2000), or re-constructed using palaeoecology (e.g. van Bellen et al., 2018), with all the uncertainty that entails. Peatlands which have undergone artificial modification of water table offer a valuable opportunity to study long-term changes (Strack et al., 2006). There are many records from drained peatlands where the surface vegetation and peat has been destroyed, for agriculture, mining or forestry, but these can hardly be considered suitable analogies for natural peatlands in a drying climate and thus are not considered further. Currently, only three records exist from sites where the water table alone has been modified (Chimner et al., 2016; Minkkinen et al., 2018) without the removal of vegetation or other major modification. Chimner et al. (2016) relied on space for time substitutions for the effect of WT modification while Minkkinen et al. (2018) relied on the comparison with natural peatlands in the literature. Both Minkkinen et al. (2018) and Chimner et al. (2016) showed their dry sites to have retained CO_2 sink function, though annual NEE was close enough to zero that it is uncertain whether these sites would be carbon sinks when the total carbon balance, including loss of carbon via aquatic and methane pathways, is considered. The dry site in Chimner et al. (2016) appeared to show a decline in sink strength, relative to the reference site. However, no estimate of flux error is included, and the difference of 48 g C m^{-2} between dry and reference is within what could reasonably be construed to be within eddy covariance flux error (50 g C m^{-2} in Baldocchi, 2003). It is notable that for the sites discussed in Chimner et al. (2016) there are very few differences in plant composition despite the different water table regime. For instance, the ericoid shrub *Chamaedaphne calyculata* appeared to dominate both the wet and the dry site in terms of biomass production, only the moss *Sphagnum fuscum* appeared to differ, being present in the reference site but

not the wet or the dry. Thus, the results of Chimner et al. (2016) may indicate a decline in NEP for the dry site, but if real, it is minor and has occurred without major changes to vegetation. A similar situation is presented in Minkkinen et al., (2018), with little to no change in the peat vegetation and NEP within a plausible range compared to pristine sites.

While ecosystem-scale eddy covariance measurements in drying peatlands are rare, considerably more literature exists outside of the EC field. Therefore, it is pertinent to consider work done on this topic utilising other techniques, recognising the strengths and weaknesses of each approach. These broadly fall into two categories: contemporary studies, following either a chamber or mass-balance approach, or palaeoecological studies which provide information on peat accumulation and biogeochemical changes over long time periods. Chamber approaches, and usually mass balance approaches as well, are useful for looking at the small-scale response of peatland carbon to environmental forcing, but fail to integrate larger scale-dependent processes which are an important consideration of peatland response to the water table (Holden, 2005; Eppinga et al., 2008). Palaeoecological approaches are generally spatially limited to one or two sites in the bog and can, therefore, provide a misleading picture of the behaviour of the sites as a whole. Additionally, the greater uncertainty of past climate, combined with low temporal resolution makes it difficult to study specific processes and influences, but these measurements instead have the advantage of capturing the net result of these processes and the influence of long-term feedbacks.

2.7.2 Chamber measurements of CO_2 flux following long term water table lowering

A number of authors (e.g. Laine et al., 2007; Maanavilja et al., 2011; Schneider et al., 2012; Waddington and Roulet, 1996) have used flux chambers to investigate differences in CO_2 flux across different microtopographic locations within bogs to determine the effect of long-term water table position. While this approach is not fully analogous to an ecosystem-wide drawdown of the water table, neglecting scale-dependent processes, it does provide an indication of the direction of change in C fluxes which may be expected if the relatively dry microsites are to become more predominant. The results of these studies are mixed. Maanavilja et al. (2011) and Schneider et al. (2012) found greatest CO_2 uptake in the hollows, while

Waddington and Roulet (1996) found the opposite with greatest CO_2 uptake in the dry microsites. Laine et al., (2007) found CO_2 uptake to have an optimum at water table depths of around 100 mm, with reduced CO_2 uptake in wetter and drier locations. Munir et al., (2015) found greatest CO_2 uptake to alternate between hummocks and hollows, with greater uptake in the hollows under cool and wet years and hummocks during warm and dry, and indeed nutrient flows across microtopographic sites are highly dependent on climate (Eppinga et al., 2010).

Strack et al. (2006), Munir et al. (2015) and Kangas et al (2014) did something rather different, comparing not only individual microforms but also drained and undrained sites. Munir et al. (2015) investigated recently drained (1-3 years) and older drained (10-13 years) sites. Both Strack and Munir found drainage to decrease the CO_2 sink, with Munir's recently drained site becoming a source, compared to the long-term which was a reduced sink. The hollows were generally more affected by the drainage than the drier hummocks, becoming large sources, whereas the hummocks were both less affected by the drawdown and appeared to recover their C sink in the long-term drained site. This differs from the findings of Strack et al., (2006), who found hummocks to become a source for CO_2, and no significant change in wetter microforms. Kangas et al., (2014) found no difference in the photosynthetic properties of mosses in drained and undrained sites, however, the difference in the water table was very small, less than 100 mm. In another approach to the problem, Gatis et al., (2016) measured CO_2 fluxes along a transect leading away from a drainage ditch, which was at least 16 years old and probably much older. No significant difference in CO_2 fluxes was found, although, the difference in mean water table depth was again very small, only 60 mm.

2.7.3 Mass balance

In addition to measuring CO_2 response using chambers and eddy covariance, others have adopted a mass balance approach, where decay and productivity are measured or estimated for example (Straková et al., 2012; Mäkiranta et al., 2017; Korrensalo et al., 2018). Earlier work, such as that of (Clymo and Reddaway, 1971) and (Malmer and Wallen, 1999) again focused on microtopographic differences in growth rates.

Straková et al. (2012) found large differences between short-term water table drawdown (4 years) and long-term water table drawdown (40 years) with

enhanced biomass production compensating for enhanced decay in the site, allowing for 2 years of aerobic decay, undergoing long-term water table drawdown and relatively minor differences between the pristine and short-term site, mostly due to inputs from trees. Korrensalo et al. (2018) in contrast, for a treeless bog, found no significant difference in biomass production along with a gradient of long-term water table position, noting that the water table optima for species along the gradient differed. Likewise, Mäkiranta et al. (2017) found no significant difference in biomass production with a 30-70 mm drawdown in the water table but did record a shift away from moss and towards shrub dominance. Bridgham et al. (2008) took a more experimental approach compared to other mass balance approaches using peat mesocosms, manipulating water table depth and observing changes in carbon stocks over a period of 8 years. His results were surprising, with the 'dry' bog, previously adapted to mean water table of 250 mm rapidly accumulating carbon, as much as 332 g C m^{-2} yr^{-1} upon raising the water table depth to 20 mm, compared to wet fen peat which rapidly lost a large amount of carbon, as much as 800 C g m^{-2} yr^{-1} in response to water table lowering from +20 mm to -250 mm. The end result was that the water table returned, or came close to returning to its initial starting point, either by rapidly gaining peat height in the bog, or rapidly losing peat in the fen through oxidation and consolidation.

2.7.4 Palaeoecology

A considerable body of literature exists around the response of peatlands to climatic changes in precipitation in the past. Some of the earliest investigations into peatlands noted changes in peat stratigraphy, for instance, the short-lived presence of 'bog oaks' in blanket peat (Aiton, 1805) and correctly interpreted them as indicative of drying, as later confirmed by Gear and Huntley (1991). Palaeoecological investigations of peatlands, following the modern scientific method, have been ongoing for nearly a century, with modern scientific investigation commencing with the demonstration of fossil pollen analysis to the Swedish Society for Anthropology and Geography in 1916 by Lennart von Post (Edwards, 2018). Students of von Post spent much of the early 20th century examining peatlands worldwide, including Scotland (Erdtman, 1924a) and New Zealand (Erdtman, 1924b; Cranwell and von Post, 1936). Compared to flux based investigations, the palaeoecological approach has the advantage of more numerous records, spanning a greater diversity of peat types and a wider

geographical area. For instance, in the UK, there are over 475 dated records of peat accumulation, published post-1970 (Payne et al., 2016) distributed across all major peat types and peat-forming areas, compared to only four eddy covariance sites with published data spanning more than a year (Helfter et al., 2015; Levy and Gray, 2015; Hambley et al., 2019). Similarly, in New Zealand there are two eddy covariance records from peatlands, Moanatuatua and Kopuatai bog (Campbell et al., 2014; Goodrich et al., 2015) considered also in this thesis, yet a considerable number of palaeo-records exist from New Zealand peatlands spanning a considerably more diverse range of peat types and geographical locations including Northland (Elliot, 1998; Newnham, 2012; Dodson and Enright, 2014), Waikato (Cranwell, 1953; Harris, 1963; Lambert, 1970; McGlone et al., 1978; Newnham et al., 1995; Jara et al., 2017) the central axial mountains (Moar, 1956, 1961, 1967), Taranaki (Mc Glone and Neall, 1994), Hawke's Bay (Mcglone, 2002), the South Island (Moar, 1970, 1973; Dodson, 1978; Wilmshurst et al., 2002) and the Chatham Islands (Dodson, 1976; Mildenhall, 1976, 1994). In this section, we will discuss then summarise the information which can be gained from these analyses. We will first of all focus on records from New Zealand, where the work carried out in this thesis is to take place, before returning to the global scale and contextualising the place of New Zealand peatlands within the global literature.

2.7.4.1 New Zealand

New Zealand peatlands are generally much older than those in the Northern Hemisphere, as much of the North Island was not glaciated during the last glacial maximum. As such palaeoecological records from New Zealand peatlands are of global significance, spanning a longer climatic period than many Northern Hemisphere peatlands and containing a record of response to a greater degree of climatic variation that is typically seen in palaeoecological records from peatlands. For example, the oldest record in the UK dates back to 12,450 BP (Hughes et al., 2000; Payne et al., 2016) compared to 29,300 BP in mainland New Zealand (Newnham, 2012) and on Rēkohu, the Chatham Islands, peat has been dated to 33500 BP, with additional sequences which are too old for radiocarbon dating and are thought to date to the Eemian interglacial period ~150,000 BP, before the last glaciation (Mildenhall, 1994). Buried peatlands from Waikato are also suggestive of active peat accumulation during the glacial period (McGlone et al., 1978).

Palaeoecological records from New Zealand bogs have not generally focused on carbon dynamics, but there is a wealth of information on vegetation change and peat accumulation rates. This literature outlines both the resilience of New Zealand peatlands, with records persisting over a diverse range of climatic conditions, but also the vulnerability of these systems, with the accumulation record punctuated by hiatuses in peat accumulation (e.g. Elliot, 1998; Newnham, 2012) and other records displaying major changes in vegetation, such as the colonisation of deep peat with trees (Allan, 1928; Mc Glone and Neall, 1994; McGlone, 2009), and the near disappearance of major peat formers from the record (Mc Glone and Neall, 1994; Newnham, 2012). Some of the sites investigated are 'relict' with the surface sequences missing (Mildenhall, 1994) and other sites are undergoing erosion (Moar, 1956), suggesting either climate or human influences have caused peat formation to cease. Below a summary is presented of the response of New Zealand peatlands to the most significant changes in climate over the last 30,000 years as inferred from palaeoecological records.

Last Glacial Cold Period (ca. 30,000 – 18,000 cal. yr. BP)

Several records of peat accumulation on vegetation exist from around the period of the last glacial maximum e.g. (Elliot, 1998; Newnham, 2012). The climate in New Zealand was around 6 °C colder than today (Anderson et al., 2012) with much of the landscape being unable to support tree growth, being instead covered by grass and shrubland (Alloway et al., 2007). There were numerous peatlands in the north of New Zealand and Rēkohu, some of which have persisted into the present day, others such as those in the Waikato were buried by alluvial sediment (McGlone et al., 1978). The record from Rēkohu, the Chatham Islands, is too coarse to draw all but the most superficial observations but indicates that restiad plants were locally dominant for some time prior to ~34,000 cal. BP (Mildenhall, 1994). Peat initiation at Otakairangi peatland dates to 30,000 cal. yr. BP (Newnham, 2012) while Kaitaia bog, in the far north of New Zealand, is believed to have initiated around 25,000 cal. yr. BP (Elliot, 1998). After an initial phase of sedge dominance, both of these Northland peatlands display a steady increase in restiad pollen until 22,500 cal. yr. BP at Kaitaia (Elliot, 1998) and 21,000 cal. yr. BP at Otakairangi (Newnham, 2012) This occurred during a period of poor climatic certainty (Alloway et al., 2007), but with some limited evidence pointing

to a gradual shift to warmer and wetter conditions (Elliot, 1998; Alloway et al., 2007; Newnham, 2012). After this period, it is believed that both bogs underwent a major perturbation. This appears to have been synchronous with the termination of the last glacial maximum (ca. 18, 000 cal. yr. BP) which is the single strongest climatic event registered in palaeo-environmental proxies in New Zealand over the last 30,000 years (Alloway et al., 2007). This expressed itself most noticeably in an expansion of tall forests into areas which previously supported low grassland and scrub. This is regarded as being driven by warming temperatures (Alloway et al., 2007) with an increase of 6 °C in mean temperature occurring within a short space of time as estimated from the movement of glaciers (Anderson et al., 2012) and isotopes preserved within the Vostok ice core (Lorius et al., 2006). During this time, Otakairangi experienced a decline in restiad species, to the point where they become almost absent from the record, and the bog became dominated by woody *Leptospermum spp* (Newnham, 2012) while at Kaitaia peat accumulation was very slow around this time, showing a similar decline in restiad pollen, and an increase in both *Leptospermum*, sedges and charcoal consistent with warm and dry conditions. In contrast, at the Kaipo wetland, located further south at a much higher altitude, peat accumulation was initiated around this time (Alloway et al., 2007) which would be consistent with the effect of warming in a cooler, alpine environment.

Late-glacial reversal (ca. 14,000 – 11,000 cal. yr. BP)

The late-glacial reversal was a period of perceived climatic cooling in New Zealand, although this is inconsistently recorded in paleoenvironmental proxies (Alloway et al., 2007). In the north of New Zealand, this coincided with an increase in restiad species and peat accumulation at Kaitaia, while at Otakairangi there was also an increase in restiad pollen with declines in *Leptospermum* spp and sedges. There was also an increase in inundation of the peatland from floods, depositing a significant amount of clay onto the peatland. At Kaipo wetland, further south and at a higher altitude, there was a hiatus in peat accumulation for nearly 1000 years, believed to be primarily due to climatic cooling (Alloway et al., 2007). Two major areas of peatland, Kopuatai and Moanatuatua (de Lange, 1989; Hogg et al., 1987; Jara et al., 2017) initiated at this time, being very wet and sedge-dominated, with a possible lake at Kopuatai (De Lange, 1989), further south Eltham ‘swamp’ initiated at ~13,000 BP as a sedge-dominated peatland (Mc

Glone and Neall, 1994). On Rēkohu there was also a pulse of peatland initiation at ~14,000 cal. BP and existing peatlands saw a shift towards restiad dominance with declines in Poaceae and Cyperaceae (Mildenhall, 1994).

Early Holocene warming (ca. 12,000 – 10,000 cal. yr. BP)

The period of early Holocene warming marks the most significant warming event after the LGM termination (Alloway et al., 2007), the Waikato region is estimated to have undergone a 1 °C increase in mean annual temperature (Jara et al., 2017) with the New Zealand climate also becoming considerably wetter (van den Bos et al., 2018).

At Kaitaia and Otakairangi this did not appear to coincide with any major changes in the bog vegetation. While increases in tree cover were recorded in the region near Kaipo bog, changes to the bog vegetation are not clear (Lowe et al., 2000; Alloway et al., 2007). At Moanatuatua the restiads *Sporodanthus* and *Empodisma* increased in abundance along with other typical bog species (Jara et al., 2017) while smaller, isolated fens merged into a large fen wetland at Kopuatai (Newnham et al., 1995). In Taranaki, there was a shift from sedge-dominated to an *Empodisma* dominated peat-forming community (Mc Glone and Neall, 1994)

Early to mid-Holocene wet period (ca. 9,600 – 7,500 cal. yr. BP)

At Kaitaia, the highest counts of restiad pollen occurred during this time, with other bog species, such as the fern *Gleichenia spp*, declining to very low counts while no clear change was seen at Otakairangi. Kaipo does not have a published record for this time and Kopuatai was mostly flooded due to an increase in sea levels (Newnham et al., 1995). At Moanatuatua, the pollen indicators suggest the bog was the wettest it had been in its history with peak values for *Sporodanthus* and *Empodisma* (Jara et al., 2017). At Eltham swamp, the *Empodisma* dominated community declined and was replaced by swamp forest of Sy*zygium maire*, which was quickly succeeded by the tall swamp forest of *dacrycarpus dacrydioides* (Mc Glone and Neall, 1994), similarly on Rēkohu some sites saw a decline in the restiad community, which was replaced by *Dracophyllum* forest.

Late Holocene climate change

The late Holocene has been characterised by a decline in restiads at Kaitaia, with the lowest counts since the LGM termination occurring at around 3,000 cal. BP. At Otokairangi a similar pattern occurred, with *Empodisma* becoming almost

absent from the record and being replaced by *Leptospermum* and sedges. In Rēkohu, there was a further shift away from restiad dominance towards *dracophyllum* around 2,700 cal. BP (Mildenhall, 1994). The peat accumulation rate declined at Kopuatai, reaching a minimum at 1850-700 cal. yr. BP and the frequency of fire increased over the period (Newnham et al., 1995). Moanatuatua underwent cyclical patterns of *Sporodanthus* and *Gleichenia* abundance with steady declines in *Empodisma,* which stabilised after 1,500 cal. yr. BP. At Eweburn bog in the south island, *Empodisma* almost disappears from the record at around 3,000 cal. BP and is replaced by sedges (Wilmshurst et al., 2002).

2.7.4.2 International

Globally there has been considerable attention given to the topic of how peatland carbon has interacted with climate over longer timescales (Mauquoy et al., 2002; Yu, 2011; Ratcliffe et al., 2018b; Treat et al., 2019). Unlike the studies done to date in New Zealand, C accumulation has been measured directly and is not inferred from vegetation changes and or peat accumulation rates. Global records provide some surprising insights. Published records of C accumulation reveal a large degree of variation between sites. Several large compilations of Northern Hemisphere C accumulation have stressed the length of the growing season to be a major driver (Charman et al., 2013), with this in turn being driven primarily by changes in insolation, particularly at the millennial timescale. However, these studies have been highly biased towards cool peatlands in continental climates with highly contrasting summers and winters. There have been doubts cast as to whether this is valid for peatlands which do not have a continental climate and can maintain a degree of growth and CO_2 uptake year-round (Loisel and Yu, 2013a). Tropical peatlands, for instance, have shown very little sensitivity to changes in temperature throughout their history (Treat et al., 2019), while lower latitude temperate peatlands have been shown decreased peat accumulation with warmer conditions (van der Linden et al., 2014). The evidence for a hydrological influence on peat C accumulation is highly nuanced. Swindles et al., (2017) showed the same bog was capable of increased or reduced C accumulation in response to drying depending on the developmental stage, in line with the theory of Hilbert et al., (2000) and Belyea and Clymo (2001), while in two compilations of records from blanket bog in Scotland, located at varying altitudes and

topography Ratcliffe et al. (2018b) and Anderson (2002) found that a period of pronounced drying, severe enough to cause an unprecedented expansion of trees across the landscape (Gear and Huntley, 1991), resulted in an inconsistent response of peatland C accumulation between sites, with most sites showing a slowdown in C accumulation but others displaying quite the opposite trend. Some fens have been shown to accumulate C rapidly upon water table raising coinciding with climatic wet periods (Yu 2003), but others, once again, display the opposite trend (Loisel and Yu, 2013b). In other sites, hydrological change is inconsistently registered, even when it apparently produces marked changes in one site (Mauquoy et al., 2002; Langdon and Barber, 2004).

The palaeoecological evidence presents a complex picture of peatland response to climate, and is supportive of the idea that peatland carbon uptake is constrained by a climatic envelope, but highlights that within this envelope optimal conditions for carbon uptake can differ both spatially and across time. General trends are discernible, but with plenty of exceptions and highly site and time specific responses. Increasingly evidence points to long-term sensitivity of the peatland carbon balance to moisture changes only when important thresholds are passed, whereas temperature and temperature derived drivers tend to be more incremental, with smaller changes having the potential to influence the carbon sink. The inherent biases in both contemporary and palaeoecological studies, primarily towards peatlands which have survived into the modern era, but also towards those sites comfortably within the climatic envelope, places limits upon our ability to determine meaningful thresholds of climatic response.

2.8 The influence of timescale on the drivers of carbon flux

Choice of timescale is key to understanding the drivers of peatland carbon balance. Variation in meteorological drivers occurs over multiple different timescales (Baldocchi et al., 2001) and because of this, the strength of the effect of meteorological drivers on carbon flux depends on the timescale considered (Baldocchi et al., 2001), which is fundamentally a philosophical concept, but one which is necessary to consider when we think about ecosystem-climate interactions and a concept which is seldom directly addressed or justified. For instance, by analysing four years of meteorological data, (Baldocchi et al., 2001)

found solar radiation to be an important driver of CO_2 flux exchange across the 12 and 24 hour timescales, due to the daily rising and setting of the sun, but also at the synoptic timescale of 3-7 days, due to the effect of different weather systems. However, solar radiation as a driver of interannual carbon fluxes was much less relevant when compared to other drivers such as temperature. This is because the variance in solar radiation is relatively low between years, compared to both shorter timescales, and other drivers (Baldocchi et al., 2001). If this concept is extended further in time, to the millennial scale, variance in solar radiation once again becomes important (Huybers, 2006; van den Bos et al., 2018), and as such is a strong driver of C exchange in bogs at these very long timescales, albeit one that also has indirect effects (Mauquoy et al., 2008; Charman et al., 2013; Loisel et al., 2014).

Internal processes, occurring in response to low-frequency changes in the water table, such as the adaptation of the peat vegetation, and changes in peat physical and chemical properties, should be viewed in the same manner. Low variance at the sub-decadal timescale does not mean these are not powerful drivers of carbon fluxes, it simply means we are less able to assess their significance when we focus either on time periods which are too short or alternatively too long. Although it is somewhat a matter of philosophical debate, the 20 to 100-year timescale is widely accepted as the most critical for the current threat of climate change, as evidenced from the use of 20 and 100-year timescales for reporting CO_2 equivalents (Bernstein et al., 2007). However, this time period is the least well understood in terms of C dynamics (Frolking et al., 2014; Ratcliffe et al., 2018a), falling into a gap between contemporary studies, which rarely run for more than a decade, and paleoecological studies which tend to be low resolution (Typically one dating point per ~1000 years from Payne et al., 2016). There is a clear need to understand what the dominant drivers of peatland carbon exchange are over timescales which most people consider to be relevant for climate change.

2.9 Peatland response to drying at different timescales - a summary

The response of peatlands to drying is often inconsistent and contradictory between sites, regardless of time and spatial scale considered. Despite this, some general patterns can be seen. What is apparent from the literature is that a) the

previous hydrological state of peatlands is important for determining their response to drying b) the response to drying changes with time. Somewhat paradoxically, wet sites undergoing drying are more vulnerable to short-term losses of C (Table 2.2), but the literature supports the idea that they will, in fact, be more resilient to WT drawdown and even have the potential to become a stronger carbon store in the future (Hilbert et al., 2000; Belyea and Clymo, 2001). However, it should be noted that the net effect of short-term losses of C and long-term recovery of the C sink over 20 to 100-year timescales is uncertain. Drier sites are harder to interpret, they are on average less responsive to short-term water table drawdown (Table 2.2), and some dry peatlands seem to be able to function as a reduced carbon sink over long time periods, providing important ecological thresholds are not crossed (Munir et al., 2015; Chimner et al., 2016; Minkkinen et al., 2018). However the contemporary literature is not unanimous in this regard, despite evidence from eroding and marginal peatlands being sparse, and there is an indication that some sites may turn into CO_2 and thus carbon sources (Strack et al., 2006). The paleoecological record also shows that the effects of drying can be dramatic, halting or dramatically slowing peat accumulation for a period of thousands of years, this is despite an inherent bias in the palaeo-record towards peatlands which are stable (Loisel et al., 2017), and thus have survived in order to be studied in the modern time period.

It is notable that most contemporary investigations thus far have looked at peatlands where changes in long term water table position have been insufficient to cause major changes in vegetation, which is contrary to both what is observed and predicted. The expansion of woody shrubs is common with especially pronounced drying, yet it is not known if this is a mechanism for the resilience of the carbon sink or a sign of instability (Waddington et al., 2015).

There are still large gaps in our current understanding of drivers which are important for peatland carbon cycling at the decadal to centennial timescale in different peat types. These gaps have led to models built using relationships between environmental variables and carbon fluxes, gained from shorter or longer timescales, being applied to a time period where we know very little about the drivers of carbon balance, with contradictory results.

The knowledge gaps are most pronounced spatially at the ecosystem-scale, and temporally at the decadal to centennial timescale, where there have only been a

small number of studies, with less than ideal ‘control’ (space for time, literature comparison), with control being used in a loose sense to refer to a ‘baseline’ or pristine reference site. Most notably there is almost nothing known in the contemporary literature about change in carbon balance for dry peatlands which undergo further drying, sufficient to cause an increase in shrub cover.

2.10 Non-hydrological drivers of C accumulation at decadal to centennial timescales

In addition to drying, peatlands are experiencing increased disturbance, such as fire, elevated CO_2, and alterations in nutrient inputs. Fire and nutrients are to a large extent interrelated (Dikici and Yilmaz, 2006; Depante et al., 2018), with fires promoting growth through nutrient related effects long after a fire event (Ward et al., 2007; Wieder et al., 2009) and there is debate in the literature as to the net effect on carbon stocks (Turetsky et al., 2015; Heinemeyer et al., 2019).

Evidence of human activity can be found preserved in archives even in the most remote parts of the globe (e.g. Turney et al., 2018) and this has led to calls for the definition of a new geologic epoch, the Anthropocene. During the 20th century, and especially after the 1945 “great acceleration” there have been major changes to global nutrient cycling (Steffen et al., 2015). For example, peatlands across large geographical areas, such as Ontario, Canada (Turunen et al., 2004) and southern Sweden (Sundström et al., 2000) have undergone a switch from N to P limitation during the 21st century due to enhanced N deposition. Meanwhile some of the most remote peatlands in the UK are undergoing N deposition at several times the historical rate, and at levels found to influence vegetation communities (Payne, 2014).

For a long time, the atmospheric component of the global phosphorus cycle was assumed to not have been impacted by human disturbance, due to P not having a gaseous form which is common in the environment. However, recent research has found large increases in particulate P from combustion (R. Wang et al., 2015) and land use (Brahney et al., 2015, 2019) which have had broad geographical impacts (McTainsh and Strong, 2007), with processes such as desertification and agricultural intensification impacting ecosystems both locally and even those on other continents (McTainsh and Strong, 2007; Brahney et al., 2015). There is evidence of increased atmospheric dust affecting the nutrient status of remote

alpine lakes and causing algal blooms in formally oligotrophic parts of the ocean (Bhattachan and D'Odorico, 2014; Brahney et al., 2015). Oligotrophic peatlands have been cited as one of the most likely ecosystems to be impacted by changes in the global phosphate cycle (Tipping et al., 2014), and the highest level of phosphate deposition are typically in sites close to or adjacent to intensive agriculture (Tipping et al., 2014). Yet there has been surprisingly little attention given to the role phosphate enrichment could play in peatland C cycling.

It is claimed that in New Zealand a higher proportion of phosphate is dropped by plane or helicopter than any other country in the world and aerial topdressing as it is termed is common in the hilly parts of the North Island where commercial forestry and livestock grazing dominate the landscape (John Maber, 2008) and high fertiliser drift due to aerial topdressing has been found to alter the nutrient dynamics and successional ecology of New Zealand forests located less than 30 km from one of our study sites (Stevenson, 2004). Restiad peatlands are known to be phosphorus limited (Clarkson et al., 2005) and other phosphate-limited peatlands display increases in primary productivity concurrent with increased P inputs (Aerts et al., 1992; Sundström et al., 2000). Remote sources of atmospheric dust, from Australia, have also increased (Brahney et al., 2019) and this increase is attributed to increased agricultural intensification there (Brahney et al., 2019). These are likely to impact phosphate cycling in New Zealand, yet the mineral composition of dust inputs in New Zealand is yet to be measured.

Peatlands in New Zealand and many others elsewhere in the world have undergone an increase in burning in recent years. Burning peatlands is known to increase nutrients such as P in the surface layers and in New Zealand this was part of the process of "breaking in the land" or converting it to pasture (Aston, 1917; Reynolds, 1917; Robinson, 1938; McCraw, 1979) and often these fires would spread into intact parts of the bog (Clarkson, 1997). These nutrient-mediated effects on plant communities and plant growth can persist for a long time, for example, 75 years in Wieder (2009). Therefore nutrient dynamics in peatlands in the Anthropocene are more likely to be elevated than in the past and this will be especially true for those with a history of anthropogenic burning or those located close to major population centres and agricultural land.

2.11 Conclusion

Peatlands store a massive amount of carbon and their proven response to climate and external drivers means there is a pressing need to understand how they will respond to these drivers during the 21st century. Much of the previous research into carbon cycling in peatlands has either focused on time periods which are short (i.e. sub-decadal) or long (multi-centennial to millennial) and despite being complementary in their strengths and weaknesses both fields of literature are poorly read and cited by the other. A knowledge gap exists at the multi-decadal to centennial timescale and there have been repeated attempts to fill this gap using models derived from either much shorter or much longer timescales, with outcomes so conflicting that the reader may pick and choose any number of models and outcomes to suit their particular purposes. Such modelling approaches are arguably so flawed as to be almost meaningless and will only serve to impede further understanding of peatland C dynamics unless they are constructed using data and relationships from appropriate and relevant timescales.

After reviewing the literature, it is clear that further empirical investigations into peatland C cycling need to consider 1) the drivers that are likely to be important over the 21st century 2) how adequate variance in these drivers can be captured, for instance though appropriate timescales and resolution of measurements, and 3) whether the ecosystem response is also captured. These are not easy considerations to be made, yet sites which are anthropogenically impacted by drying or nutrient enrichment may be used as analogues for peatlands in the 21st century. In this thesis, we will focus on the impact of a sustained lowering of a peatland water table and will also investigate the impact of nutrient enrichment on C accumuation caused by past volcanic eruptions, to serve as an analogy for present day nutrient enrichment which is believed to be widespread in the present day and is likely to continue to be so during the 21st century.

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Chapter Three

Water table fluctuations control CO_2 exchange in wet and dry bogs through different mechanisms

3.1 Abstract

High water tables (WT) stabilise peatland carbon (C) through the regulation of peatland biogeochemical processes. The impact of peatland WT on ecosystem function, including C exchange, alters over time, and the factors that cause some peatlands to display resilience and others to undergo degradation are poorly understood. Here we use CO_2 flux measurements, measured by eddy covariance, to compare ecosystem function between two raised bogs; one drainage-affected, with a deep and fluctuating water table and the other near-natural, with a shallow and stable water table. The drainage-affected bog was found to be a moderate sink for CO_2 (69 g C m^{-2} yr^{-1}), 134 g C m^{-2} yr^{-1} less than the near-natural bog (203 g C m^{-2} yr^{-1}). Greater ecosystem productivity has allowed the drainage-impacted bog to act as a CO_2 sink despite higher ecosystem respiration; most likely due to an increase in photosynthetic capacity caused by the expansion of ericaceous shrub cover. The tolerance of the vegetation community, particularly the main peat former *Empodisma robustum* (Restionaceae), to low and fluctuating WT appears to have been key in allowing the site to remain a sink. Despite the current resilience of the ecosystem CO_2 sink, we found gross primary production to be limited under both high and low water tables, even in a year with typical rainfall. This is best explained by the limited physiological ability of ericaceous shrubs to tolerate a fluctuating WT. As such we hypothesise that if the WT continues to drop and become ever more unstable, then without further vegetation change, a reduction in gross primary production is likely which may cause the site to become a source for CO_2.

3.2 Introduction

Peatlands provide one of the largest stores of carbon (C) in the biosphere (Yu, 2012). The persistent uptake and storage of C by peatlands since the last glaciation has sequestered between 500 and 700 billion tonnes of C (Yu et al., 2010) an estimate which can be expected to be revised upwards as large areas of new peatlands are discovered (Draper et al., 2014; Dargie et al., 2017). This large store of accumulated C is known to be vulnerable to oxidation upon water table (WT) lowering, due to either artificial drainage (Armentano and Menges, 1986), or climate-induced drying (Fenner and Freeman, 2011). A decrease in the net water balance has been observed for some major peat forming regions (Zeng et al., 2014; Long et al., 2017) part of a trend which is predicted to continue (Fekete et al., 2010). As such, climate-induced lowering of peatland WTs is likely to occur during the 21st century and beyond (Frolking et al., 2011).

WT is a key moderator of the processes that regulate C fluxes to and from peatlands (Holden et al., 2004; Gažovič et al., 2013; Goodrich et al., 2015b; Waddington et al., 2015; Strachan et al., 2016). The response of peatland C to WT lowering is known to change over time (Hargreaves et al., 2003; Laiho, 2006; Mäkiranta et al., 2009; Hommeltenberg et al., 2014) and can be modified by numerous positive and negative internal feedbacks (Waddington et al., 2015). Peatlands with a sustained lowering of WT usually undergo fundamental physical, chemical and biological changes. For instance, lowering the WT in peatlands will often lead to increased productivity in the long term by allowing the establishment of more productive and nutrient demanding plant communities (Paavilainen and Päivänen, 1995; Laiho, 2006; Straková et al., 2012; Munir et al., 2015). Similarly, peat hydraulic and chemical properties are highly dependent on WT position (Whittington and Price, 2006; Straková et al., 2010), but major changes may lag years or even decades behind the drop in WT (Holden et al., 2004; Straková et al., 2010). Crucially, peatlands will respond differently to short-term disturbance events, such as seasonal droughts and floods, compared to long term changes in hydrology (Laiho, 2006; Mäkiranta et al., 2009; Straková et al., 2012; Waddington et al., 2015; Page and Baird, 2016). Thus, drained peatlands, which have undergone adaptation to a new hydrological regime, may serve as better analogues for intact peatlands under a consistently warmer and drier climate

(Fenner et al., 2005; Strack et al., 2006). Currently, there are large gaps in the understanding of WT-time-C interactions. The response of peatland CO_2 fluxes to instantaneous changes in WT is highly inconsistent across sites and studies (e.g. Lafleur *et al.*, 2005; Sulman *et al.*, 2009; Sonnentag *et al.*, 2010; Dimitrov *et al.*, 2011; Helfter *et al.*, 2015). Site-specific response of CO_2 fluxes to WT have been attributed to the degree of WT fluctuation observed (Lafleur et al., 2005; Sulman et al., 2009; Campbell et al., 2014; Goodrich et al., 2015a; Helfter et al., 2015), the physical and chemical properties of the peat (Lafleur et al., 2005; Sulman et al., 2010; Lund et al., 2015) and the differing vegetation communities present (Sulman et al., 2009, 2010; Sonnentag et al., 2010; Dimitrov et al., 2011; Helfter et al., 2015). All of these explanatory factors are in turn strongly affected by long-term WT position (Laine et al., 1995; Price et al., 2003; Laiho, 2006; Straková et al., 2012; Waddington et al., 2015).

In order to better understand how peatlands respond to *sustained* hydrological change, we compared ecosystem scale CO_2 fluxes of an intact bog to a highly modified drainage-affected bog using the eddy covariance technique. Our objective was to compare CO_2 flux and its drivers at the two sites. Our hypothesis being that the two sites would respond differently to environmental drivers such as light and WT, following the rationale outlined in the past section, which was that long term water table position is a key moderator of the response of peatland CO_2 flux to environmental variables. We additionally hypothesise that CO_2 sequestration at Moanatuatua will be reduced in comparison to Kopuatai, due to the exceptionally low water table at the site.

3.3 Study Site and Method

3.3.1 Study sites:

Kopuatai and Moanatuatua are both low altitude ombrotrophic restiad (dominated by Restionaceae) peat bogs located 55 km apart in the Waikato region of Te Ika-a-Māui (North Island) of Aotearoa New Zealand. Both sites fall within the fully humid, warm temperate climatic zone with warm summers, i.e. Cfb, as defined in the updated Köppen-Geiger climate classification (Kottek et al., 2006). With mean annual temperature and precipitation of 14.7 °C and 1269 mm for Kopuatai and 13.8 °C and 1121 mm for Moanatuatua (NIWA, 2017).

Kopuatai (37.39 ° S, 175.55° E, altitude 5 m), is a largely intact peatland complex ~9000 ha in size, consisting of a northern and southern dome (Irving et al., 1984), and is the hydrologically least modified of the remaining Waitako raised bogs. Any impacts of drainage are confined to the bog margins, more than 2 km from the study site and outside of the area of measurement. The main peat former *Empodisma robustum* (Restionaceae) dominates the vegetation within the measurement area comprising 85.6 % of canopy dry matter, while the two sedges *Schoenus brevifolius and Machaerina teretifolia* made up 9.7 % and the fern *Gleichenia dicarpa* constituted the remaining 4.8% (Keyte-Beattie, 2014). Towards the edge of, and beyond the measurement area, stunted shrubs of *Epacris pauciflora* (Ericaceae) and *Leptospermum scoparium* (Myrtaceae) can also be found, along with the late successional *Sporadanthus ferrugineus* (Restionaceae) which is common elsewhere in the bog.

Moanatuatua (37.92 ° S, 175.37 ° E, altitude 65 m) was originally ~7500 ha in size, comparable to modern day Kopuatai (Clarkson et al., 2004) now only 140 ha remains with peat-forming vegetation, less than 2% of the original extent. The remainder has been converted to agricultural land (Clarkson et al., 2004). Drainage and land conversion began in earnest in the 1930s (Cranwell, 1939) and by 1974 the remaining bog had been reduced to its current size (Matheson, 1979). Monthly measurements of WT carried out between December 1976 and November 1977 revealed the WT to be close to the peat surface, ranging from 80 mm depth in spring to 380 mm in autumn (Matheson, 1979), this is consistent with earlier anecdotal observations of a WT at or close to the surface (e.g. Cranwell, 1939; Campbell, 1964). Modern data suggest a dramatic decline in WT depth relative to 1977 (e.g. a summer low of 813 mm repeated by Campbell *et al*, 2014 in April 2000).

The present-day vegetation community has altered relative to conditions before the drop in WT, for example with the loss of lycopod, orchid and liverwort species and the expansion of the shrub *E. pauciflora* (de Lange et al., 1999), previously described as a minor component of the vegetation community (Campbell, 1964). *Epacris pauciflora* is now co-dominant along with the restiad peat formers *E. robustum* and *S. ferrugineus*. A transect of quadrats across the measurement area in February 2017 (data not shown) revealed *E. robustum* to be the dominant species with 54.4 % ± 7.1 % cover, followed by *E pauciflora* (13.8

± 4.3%) and *S. ferrugineus* (6.6 ± 6.7%). Maximum vegetation height was 2.56 ± 0.12 m. Further information on, and a cross-site comparison of vegetation at Moanatuatua and Kopuatai can be found in Clarkson et al., (2004).

3.3.2 CO_2 flux and ancillary measurements:

Eddy covariance measurements of CO_2 fluxes at both sites were carried out simultaneously over a two year period from 1st of May 2015 until 30th of April 2017 using open path infrared gas analysers (IRGA; LI-7500, LI-COR Biosciences, Lincoln, USA) coupled with sonic anemometers (CSAT3, Campbell Scientific Inc., Logan, UT, USA). Instruments were mounted at 3.75 m above the peat surface for Moanatuatua and 4.25 m for Kopuatai, above a maximum canopy height of 3 m at Moanatuatua and 0.6 m at Kopuatai. Raw measurements were made at 10 Hz and were complemented with the environmental variables, sampled at 0.1 Hz and are described in Table 3.1)

Table 3.1. Additional measurements of environmental variables at Moanatuatua and Kopuatai.

Variable	Moanatuatua Instrument	Kopuatai Instrument
Photosynthetic photon flux density (PPFD)	BF5, Delta-T, UK	BF5, Delta-T, UK
Water table level (WT)	WL1000W, Hydrological Services, NSW, Australia	WL1000W, Hydrological Services, NSW, Australia
Net shortwave and longwave radiation	NR01, Hukseflux, Netherlands	NR01, Hukseflux, Netherlands
Surface temperature	NR01, Hukseflux, Netherlands	NR01, Hukseflux, Netherlands
Air temperature	HMP 155, Vaisala, Finland	HMP 155, Vaisala, Finland
Humidity	HMP 155, Vaisala, Finland	HMP 155, Vaisala, Finland
Rainfall	TR-525M, Texas Electronics, USA	TB5, Hydrological Services, Australia

3.3.3 Flux terminology and data handling

The CO_2 flux terminology recommended by Chapin et al., (2006) has been adopted. Net ecosystem production (NEP) was defined as the difference between

gross primary productivity (GPP) and ecosystem respiration (ER). For NEP, positive values indicate an ecosystem CO_2 sink while negative values a CO_2 source. GPP and ER are always positive. Net ecosystem exchange (NEE) is used for 30-minute periods and uses the opposite sign convention to NEP, with negative values representing an ecosystem CO_2 sink.

Half-hourly CO_2 fluxes were calculated from high-frequency data using the EC software EddyPro™ 6.2.0 (LI-COR Inc., USA). The effects of air density fluctuations were compensated according to Webb *et al.* (Webb et al., 1980). Fluxes associated with low friction velocities, below 0.07 ms^{-1} for Kopuatai and 0.09 ms^{-1} for Moanatuatua, were rejected following the u_* threshold detection method described by Reichstein et al. (2005). Tower-level CO_2 fluxes were corrected for CO_2 storage in the air and vegetation layer beneath the EC sensors using average CO_2 concentrations measured by the LI-7500. Spikes in the high-frequency raw data were detected and removed, and additional tests for amplitude resolution, dropouts, skewness and kurtosis were carried out following Vickers & Mahrt (1997). Corrections for high-pass and low-pass filtering effects (e.g., flux losses due to detrending, sensor separation, and time response) were performed (Moncrieff et al., 1997, 2004). Fluxes were quality flagged using the EddyPro flags adapted from Mauder & Foken (2004). With the criteria ranging from best (0) to bad (2). All fluxes flagged with "2" were rejected. Fluxes flagged with "0" and "1" were used for partitioning NEE into GPP and ER, and calculating gap-filled daily and longer-term totals. Only fluxes flagged with "0" were used for light response analysis and direct comparison on NEE and WT.

After flagging, remaining CO_2 flux values greater than 15 μmol m^{-2} s^{-1} and below -20 μmol m^{-2} s^{-1} were deemed implausible for these ecosystems and were removed. The datasets were then filtered for soft spikes using a 14-day moving window. Fluxes which deviated more than 2 standard deviations from the mean for that half hour period, and flagged more than twice, were eliminated as the window moved through the dataset. The total CO_2 flux data remaining, including gaps where the instruments were offline due to technical failures, was 50.6% for Kopuatai and 39.1% for Moanatuatua. For night time data this dropped to 36.8% and 25.2% respectively.

The flux footprints were modelled using the technique of Kljun et al. (2004), providing an estimated 90% footprint radius of 683 m at Kopuatai and 82 m at

Moanatuatua. This decreased to 567 and 77 metres for "0" flagged data, which excluded moderate quality data used for gap-filling.

Gap filling for annual and monthly estimates of NEP was carried out by applying the artificial neural network (ANN) technique (Papale and Valentini, 2003; Moffat et al., 2007; Goodrich et al., 2017) using Matlab code created by Cove Sturtevant (Biometeorology Lab, University of California Berkeley). Two models were used, one for day-time conditions, the other for night-time. Both models used fuzzy variables for season and year (Papale and Valentini, 2003) and shared inputs of surface and air temperature along with vapour pressure deficit (VPD) and water table depth. The day-time model had an additional input of photosynthetic photon flux density (PPFD), while the night-time model used inputs of wind speed and temperature lagged by four hours, with the rationale that this will influence the temperature of the canopy and upper peat layers. Yearly estimates of NEP were produced from the sum of individual gap-filled half-hour periods.

3.3.4 Uncertainty analysis

Uncertainty analysis was carried out following the methods described by Elbers et al., (2011). This included uncertainty around the selection of the u_* threshold and statistical screening in addition to measurement error and flux calculation uncertainty, the latter two being estimated using the technique described by Dragoni et al., (Dragoni et al., 2007). We did not include the LI-7500 self-heating correction, as this was not necessary due to the warm climate at our field sites (Figure 3.1). In order to estimate the uncertainty around the selection of the u_* threshold we re-processed data using u_* threshold values 0.05 m s^{-1} above and below the chosen value (i.e. u_* of 0.04 m s^{-1} and 0.14 m s^{-1} for Moanatuatua and 0.02 m s^{-1} and 0.12 m s^{-1} for Kopuatai). Error from statistical screening was estimated by altering the threshold of error detection in the moving window filter by ± 0.5 times the standard deviation (i.e. 1.5 σ and 2.5 σ). Measurement error was estimated using paired observations from one site separated by 24 hours, under similar conditions (successive days approach), this was used to produce 10 000 Monte Carlo simulations of half-hourly data to provide an estimate of the error in annual measured NEP. These simulated values of NEP were then fed through the ANN gap filling model to estimate the error in the gap-filled annual NEP total. The total error was calculated as

$$\chi t = \sqrt{\chi^2 a + \chi^2 b + \chi^2 c + \chi^2 d}$$

Where χ_a is the measurement error and flux calculation uncertainty, χ_b is the u* threshold uncertainty χ_c is the statistical selection uncertainty and χ_d is the gap-filling uncertainty.

3.3.5 Flux partitioning

Night-time NEE (defined as time periods where PPFD < 20 μmol m^{-2} s^{-1}) was taken to be equivalent to ER, with GPP set to zero. Daytime ER, were then modelled by applying the night-time ANN using daytime drivers (Goodrich et al., 2017; Oikawa et al., 2017). GPP was recalculated as NEE-ER. This method is known to perform equally well compared to other standard approaches, for example, that of Reichstein et al. (2005), but may overestimate ER and GPP by 10-13% (Oikawa et al., 2017). Un-conventional techniques such as isotope partitioning (Oikawa et al., 2017), or carbonyl sulphide derived GPP (Asaf et al., 2013) remain technically challenging and thus were not used. We therefore, exercised caution in interpreting the absolute values of the partitioned fluxes. Annual estimates of GPP and ER were produced by summing the half hourly periods, composed of modelled and measured data for ER and entirely modelled data for GPP.

3.3.6 Ecosystem response to light

To investigate photosynthetic properties at the two sites and better compare with peatlands globally, the light dependence of daytime NEE was described across seasons using the Michaelis-Menten rectangular hyperbolic function derived from 30-min observed data. Seasons were defined as Spring: September to November, Summer: December to February, Autumn: March to May and Winter: June to August.

Equation 1: $$NEE = \frac{\alpha.PPFD.GPmax}{\alpha.PPFD + GPmax} + ER_0$$

Where α is the initial slope of the light response curve at low light (photosynthetic efficiency); GPmax is photosynthetic capacity, and ER_0 is ecosystem respiration at PPFD = 0 (y-intercept).

3.4 Results

3.4.1 Weather, climate and water table

Weather conditions were broadly similar across the two sites (Figure 3.1). Only minor differences in air temperature occurred, with Kopuatai 0.4 °C warmer on average throughout the measurement period. Differences in precipitation were more pronounced with Kopuatai wetter in the autumn and early-winter (Figure 3.1). The first year of measurements was warm, 0.4 °C to 1.0 °C above average, with near-normal annual rainfall at both sites. (NIWA, 2017). The second year of measurements was also warm, 0.3 °C to 0.5 °C above normal, and unusually wet with anomalously high rainfall occurring in the late summer and autumn. This lead to annual rainfall 132% and 126% of normal for Kopuatai and Moanatuatua respectively (NIWA, 2017).

The two sites had highly contrasting WT regimes (Figure 3.1), so much so that the ranges of the WT did not overlap at any point in the measurement period, i.e. the deepest WT at Kopuatai was still shallower than the shallowest WT at Moanatuatua. Both sites displayed a seasonal pattern in WT fluctuation, but this was much more pronounced at Moanatuatua, with a WT range of 704 mm compared to 230 mm at Kopuatai. Both sites experienced a gradual drop in WT from December 2015 (early-summer) onwards with the drop much more pronounced at Moanatuatua. Reaching a low of 943 mm below the peat surface compared to 170 mm at Kopuatai, despite relatively typical rainfall during the 2015–2016 measurement period (97.5 % of normal). The shallowest WT depths were recorded after heavy rain in late April 2017; at Kopuatai the WT was 60 mm above the peat surface, while at Moanatuatua the WT was 239 mm below the peat surface.

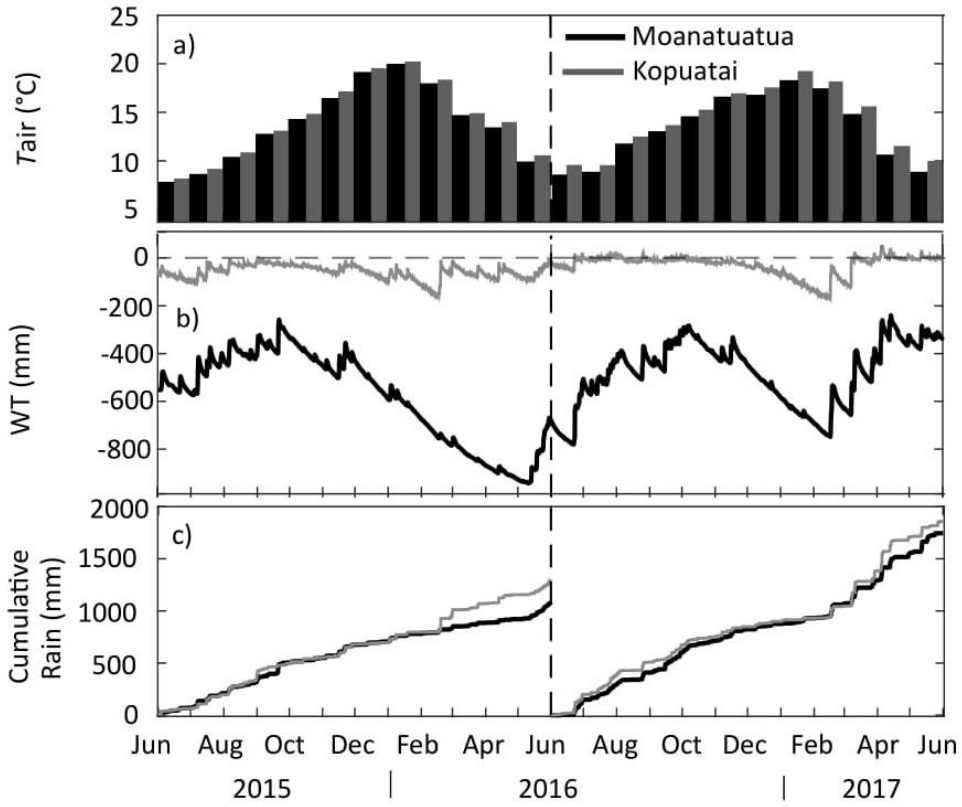

Figure 3.1 Monthly mean air temperatures (T_{air}, a) water table (WT, b) and cumulative annual rainfall (c) at Kopuatai and Moanatuatua

3.4.2 Light response of NEE

The seasonal light response of daytime NEE differed substantially between the two bogs (Figure 3.2). Large differences were seen in GPmax and ER_0 which were both between 55% and 72% greater at Moanatuatua depending on the season (Table 3.2). Both sites displayed seasonality in GPmax and ER_0 which, during summer, were more than 30% and 50% greater at both sites compared to other seasons respectively. Photosynthetic efficiency under low light conditions, α, was comparable between sites and ranged between 0.02 – 0.05 mol CO_2/mol photons (Table 3.2) and was highest in both summer and winter, with autumn and spring values were reduced.

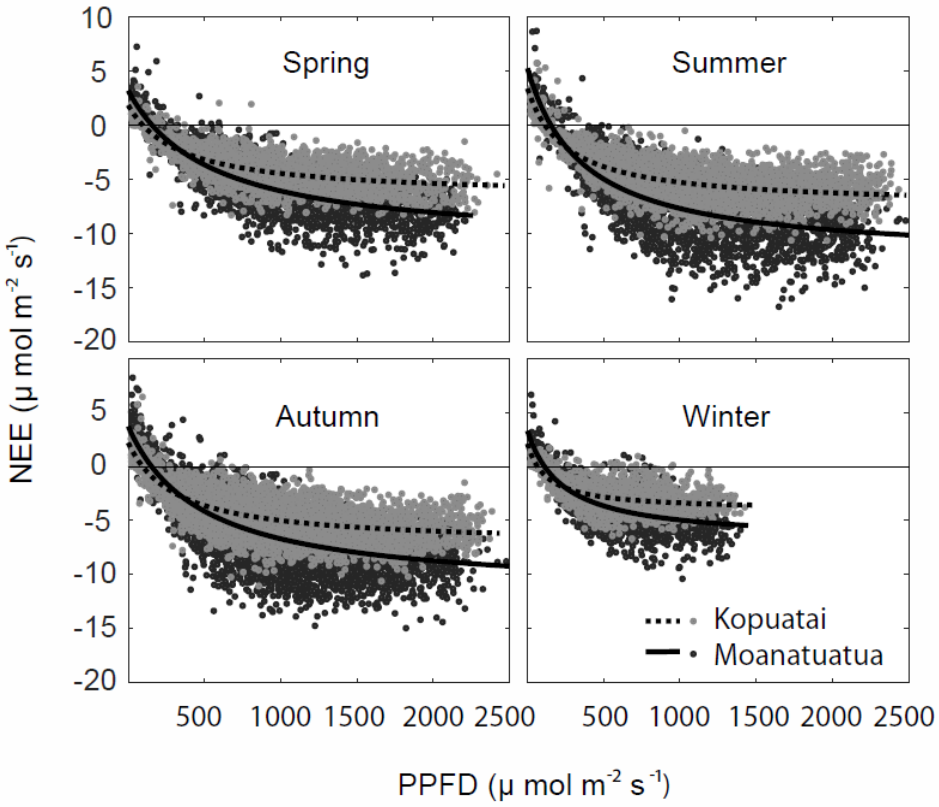

Figure 3.2. Light response curves for Kopuatai and Moanatuatua. Curves were fitted to 30-minute NEE (points) displayed in the background with Kopuatai and Moanatuatua. Seasons were defined as the following: Spring: Sept - Nov. Summer: Dec - Feb. Autumn: March - May. Winter: June - August.

Table 3.2. Light response parameters from Moanatuatua and Kopuatai. GPmax and R0 have units of µmol m−2 s−1 and α has units of mol CO2/mol photons

Parameter	Spring	Summer	Autumn	Winter
		Moanatuatua		
α	0.03	0.05	0.03	0.04
GPmax	14.3	17.6	15.5	10.2
ER_0	3.2	5.3	3.8	3.3
		Kopuatai		
α	0.03	0.04	0.03	0.05
GPmax	8.5	10.8	9.5	6.2
ER_0	1.9	3.4	2.2	2.1

3.4.3 Response of NEE to water table

To examine the effect of WT on CO_2 flux NEE was compared to WT depth, under high light conditions for both sites (Figure 3.4). Moanatuatua displayed a

parabolic response to WT depth. Half hourly measurements are inherently noisy, but when NEE is binned by increments of WT, the trend becomes more apparent. The greatest CO_2 uptake, -8.7 μmol m^{-2} s^{-1} to -9.0 μmol m^{-2} s^{-1}, as shown by the binned median occurred between -550 mm and 800 mm. Outside of this range, NEE was reduced to -6.8 μmol m^{-2} s^{-1} when the WT was shallower than 400 mm and between -8.2 μmol m^{-2} s^{-1} and -7.4 μmol m^{-2} s^{-1} for WTs deeper than 800 mm. In contrast, very little variation was seen in the binned median values for Kopuatai which varied between -5.1 μmol m^{-2} s^{-1} and -5.8 μmol m^{-2} s^{-1} with no consistent pattern across WT depths.

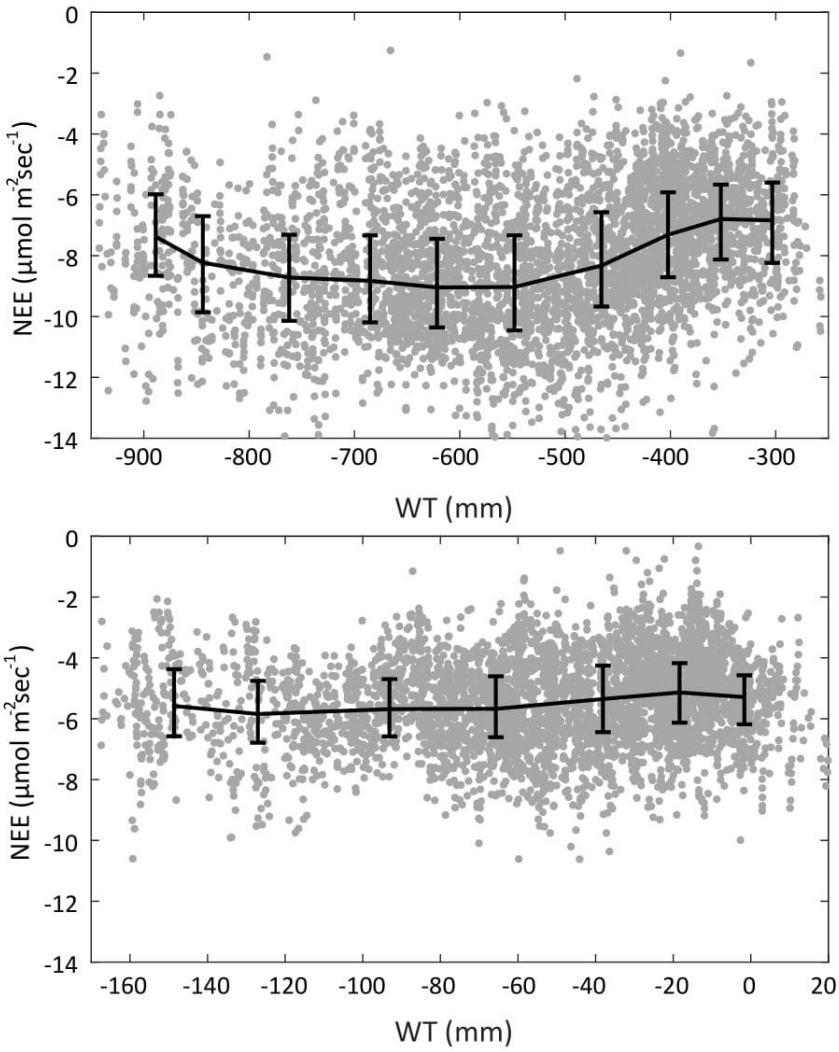

Figure 3.3. NEE binned by WT with error bars representing the interquartile range, plotted against WT depth for a) Moanatuatua (75 mm bins) and b) Kopuatai (30 mm bins). 30-minute NEE (light grey points) displayed in the background. Only NEE flagged as best quality (0 flagged), and under high light conditions (PPFD > 1200 μmol m-2 s-1) is presented.

3.4.4 Annual flux totals

Both sites were net sinks for CO_2 for both years (Table 3.3) with Moanatuatua having on average 134 g C m^{-2} yr^{-1} lower NEP compared to Kopuatai. Component fluxes at Moanatuatua were much greater than at Kopuatai, with GPP 423 g C m^{-2} yr^{-1} and ER 557 g C m^{-2} yr^{-1} greater on average. Uncertainty estimates of NEP did not overlap for the two different sites, however they did overlap across years and thus NEP was significantly different across sites, but not within sites across years.

Table 3. Summary of net ecosystem production (NEP) and component fluxes ecosystem respiration (ER) and gross primary productivity (GPP). Error bounds for NEP represent 1σ.

Site	Moanatuatua			Kopuatai		
	Year 1	Year 2	Mean	Year 1	Year 2	Mean
NEP (g C m^{-2} yr^{-1})	88 ± 26	51 ± 35	69 ± 30	192 ± 45	214 ± 40	203 ± 42
GPP (g C m^{-2} yr^{-1})	1301	1232	1266	859	827	843
ER (g C m^{-2} yr^{-1})	1213	1181	1197	667	614	640

3.4.5 Seasonal variation in fluxes

The seasonal course of cumulative NEP followed a similar pattern at both sites (Figure 3.4), with Moanatuatua displaying a greater seasonality with stronger net uptake of CO_2 in summer and greater net loss in winter. In contrast, Kopuatai remained a sink, or close to CO_2 neutral through most of each winter. The greatest divergence between the two sites occurred at different times in each year. In Year 1 this divergence occurred in late-summer, around mid-February, when Kopuatai remained a sink during autumn (28 g C m^{-2}); simultaneously a sharp drop occurred in cumulative NEP (-65 g C m^{-2}) at Moanatuatua over the autumn period (March to June), as the WT dropped below 800 mm (Figure 3.1) causing the two sites to diverge. In Year 2 the largest divergence occurred in winter when cumulative NEP dropped sharply at Moanatuatua (-73 g C m^{-2}) compared to Kopuatai where NEP remained weakly positive (7 g C m^{-2}) over the same period.

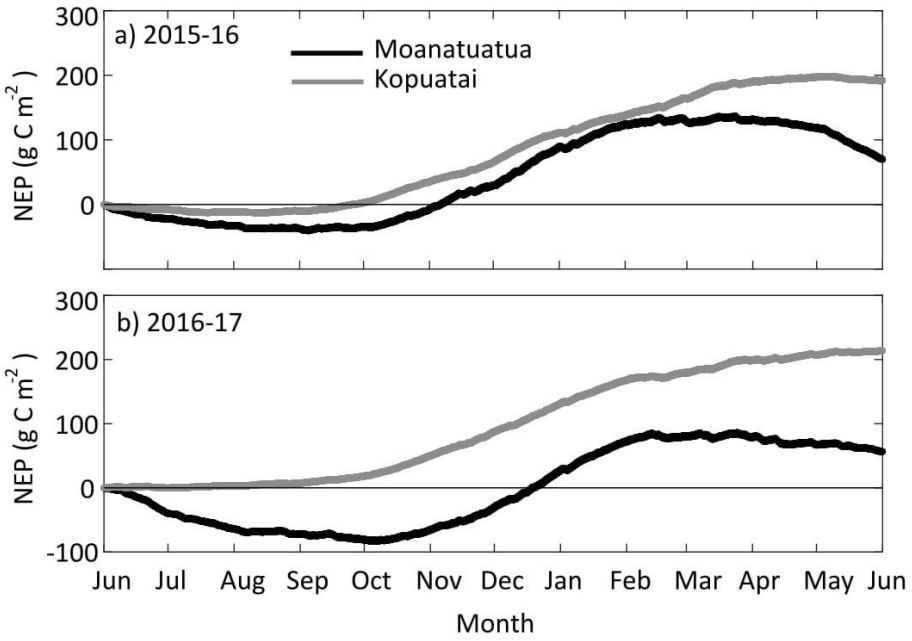

Figure 3.4. Cumulative daily NEP for Moanatuatua and Kopuatai during a) Year 1 (June 2015-May 2017) b) Year 2 (June 2016-May 2017).

Component fluxes of ER and GPP were higher at Moanatuatua than at Kopuatai for every month of the measurement period and both sites displayed broadly similar seasonal trends throughout most of each year apart from periods of divergence in the autumn (Figure 3.5). GPP peaked in late in December at both sites and then fell to approximately 33% of peak values during winter conditions in June and July. ER peaked later in the year than GPP for both sites, January in Year 1 and March in Year 2 then declined by approximately 50%, to reach minimum values between July and September.

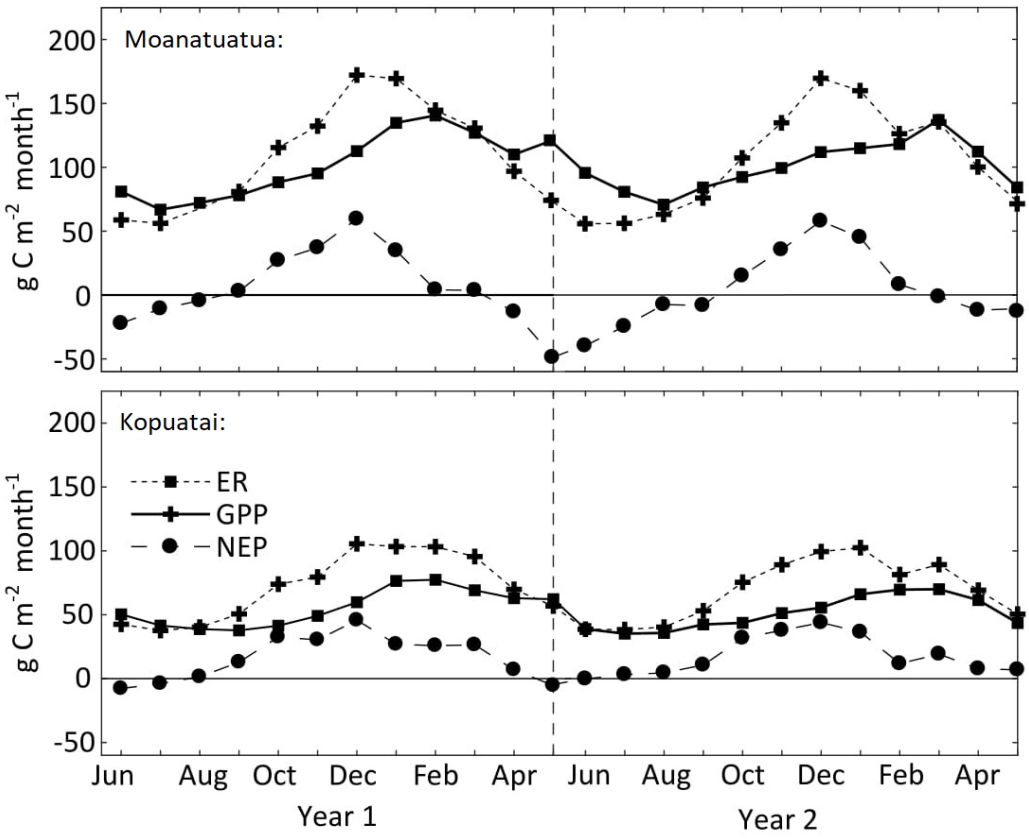

Figure 3.5. Monthly totals of ER, GPP and NEP for Moanatuatua (dry) and Kopuatai (wet) for the two years of measurement.

3.4.6 Water table and GPP

To more closely examine the role of light and WT on GPP, and the controls of temperature and WT on ER, we produced contour plots of both fluxes and their drivers. In order to avoid days with excessive gap filling, only days with more than six hours of valid daytime NEE measurements were used (Figure 3.6). In Figure 3.7 ER, air temperature and WT were plotted using median half-hourly night time ER which was measured, rather than partitioned, for nights with more than three hours of valid flux data. The lower threshold for measured data was chosen due to the lower number of valid measurements during night time conditions, which was generally due to the lack of turbulence.

The highest rate of GPP was 6.7 g C m^{-2} day^{-1} at Moanatuatua, compared to 4.1 g C m^{-2} day^{-1} at Kopuatai. The higher rates of GPP, taken to be above 6 g C m^{-2} day^{-1} for Moanatuatua and 3.5 g C m^{-2} day^{-1} for Kopuatai, occurred only when total daily PPFD was greater than 21 mol m^{-2} day^{-1}. This was possible from early-

October until late-March. In the case of Moanatuatua, maximum rates of GPP only occurred when the WT was also within an optimal range of between -400 mm and -775 mm. No such effect was found at Kopuatai where the response of GPP to WT was less clear (Figure 3.6).

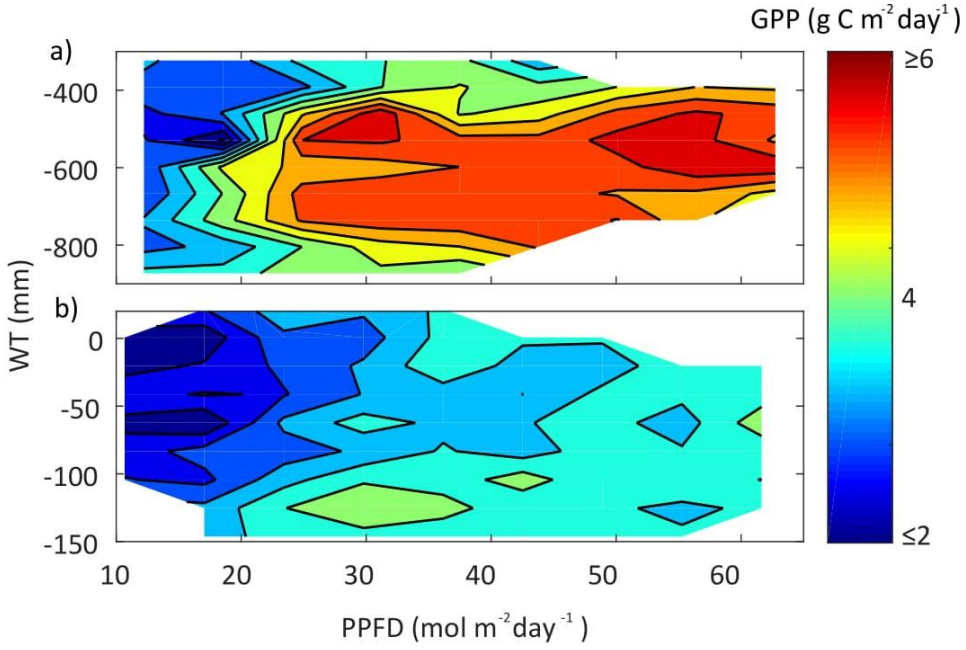

Figure 3.6. Contour plots of gapfilled GPP in response to PPFD and WT for (a) Moanatuatua and (b) Kopuatai, for days with more than six daytime hours of observed data. Contours were obtained via cubic spline interpolation. Note different scales for WT at each site.

3.4.7 Water table and ER

Maximum rates of night time median ER were much higher (8.8 μmol m^{-2} s^{-1}) at Moanatuatua with compared to Kopuatai (3.6 μmol m^{-2} s^{-1}). At Moanatuatua, rates above 4 μmol m^{-2} s^{-1} (59 days or 19% of data) were observed when mean night-time temperatures were above 14 °C (Figure 3.7). At Kopuatai the highest rates of ER (>2.5 μmol m^{-2} s^{-1}; 21 days or 7% of data) occurred when WT depths were below -140 mm and high temperatures. Variation in ER responded primarily to temperature at Moanatuatua, whereas at Kopuatai ER was driven primarily by temperature only under WT shallower than 100 mm. At Kopuatai WT was a more important driver of ER than temperature when the WT was below 100 mm (Figure 3.7); a total of 46 days during the measurement period.

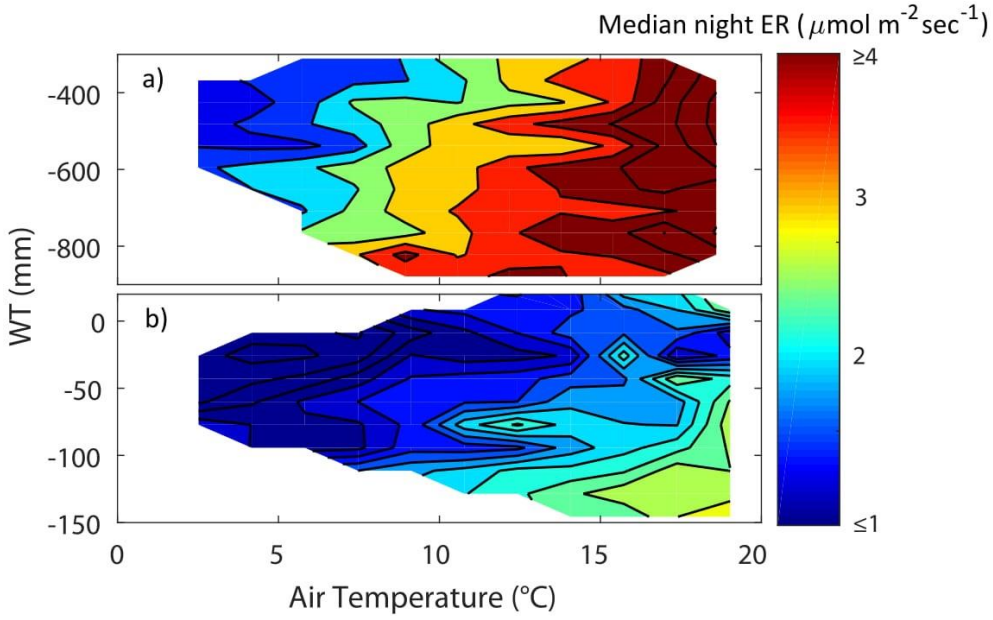

Figure 3.7. Contour plots for mean half hourly night time ecosystem respiration (ER) in response to mean night time air temperature and WT depth using observed data for nights with a minimum of 6 valid measurements. This was done for (a) Moanatuatua and (b) Kopuatai. Note that mean half hourly ER is used in preference to total night time ER to avoid seasonal changes in the length of the night time period. Contours were obtained via cubic spline interpolation

3.5 Discussion

3.5.1 Differences in flux magnitudes and totals

Both sites were annual sinks for CO_2, despite very different WT regimes. Kopuatai was a very strong sink for a peatland, with mean NEP of 203 ± 42 g C m^{-2} yr^{-1}. In contrast, Moanatuatua was a moderate sink with NEP of 69 ± 30 g C m^{-2} yr^{-1} despite the deep WT. Although NEP at Moanatuatua was reduced in comparison to Kopuatai, it remained typical of other peatlands globally, e.g. 74 g C m^{-2} yr^{-1} calculated from 24 site years across six peatlands (Lu et al., 2017). This is not the case for Kopuatai, where the sink strength was exceptionally high compared to other raised bogs (e.g. Roulet *et al.*, 2007; Strachan *et al.*, 2016). The NEP At Kopuatai was globally more comparable to treed fen conditions, for example, a fen in Alberta, Canada (189 g C m^{-2} yr^{-1} in Flanagan and Syed 2011). It should be noted that NEP at Kopuatai was consistent with previous estimates in these restiad peatlands (Goodrich *et al.*, 2017, Campbell *et al.*, 2014). It should be noted that NEP is only one component of the site carbon balance with C loss through aquatic carbon, CH_4 and biological volatile compounds comprising the remainder. Published estimates of CH_4 and aquatic C loss for Kopuatai are

available in Goodrich et al. (2017) and were found to make up 14% of the annual carbon balance.

The strong contemporary CO_2 sink strength in these restiad bogs has been attributed to relatively high year-round GPP. Light response parameters (Table 3.2, Figure 3.2) show that restiad plant communities utilise light to fix CO_2 at a rate similar to other peatlands (e.g. Frolking *et al.*, 1998; Coursolle *et al.*, 2006; Humphreys *et al.*, 2014), thus higher GPP has been attributed to a climate favourable to year-round growth, rather than a difference in how the plants utilise light (Campbell et al., 2014). It has also been found that the main restiad peatformer, *E. robustum*, decays, under warm conditions, at a similar rate to *Sphagnum spp.* under much cooler conditions (Clarkson et al., 2014) and therefore the litter of the restiad peatformers, which is enriched in lignin and other recalcitrant compounds (Kuder et al., 1998), could play a role in maintaining high NEP by suppressing CO_2 losses through ER, though this topic remains to be fully explored.

The component fluxes, GPP and ER, of the two sites (Table 3.2, Figure 3.5) were very different, despite a similar climate (Figure 3.1), suggesting fundamental differences in the way the two ecosystems respond to hydroclimatic drivers. We found that a sufficiently deep WT can reduce NEP at both bogs, but it does so through two very different mechanisms. Deeper WTs stimulated ER (Figure 3.7) at Kopuatai (hydrologically pristine) while limiting GPP (Figure 3.6) at Moanatuatua (drainage-affected). Several ecosystem traits, outlined in the following sections, allow the CO_2 sink to remain strong at Moanatuatua decades after the WT has been lowered. Our results support the idea of greater influence long-term rather than instantaneous WT changes on peatland C dynamics (Mäkiranta et al., 2009; Straková et al., 2012). While we attribute differences across sites to long term WT position, we cannot exclude the influence of long-term nutrient inputs through elevated atmospheric deposition and fertiliser drift which may be particularly relevant for Moanatuatua.

3.5.2 Gross Primary Production

Annual GPP was on average 423 g C m^{-2} yr^{-1} (50%) greater at Moanatuatua than at Kopuatai (Table 3.3). The difference between the two sites was equivalent in magnitude to the annual productivity of some peatlands (Humphreys et al., 2014).

Higher GPP occurred year-round, with the greatest differences between sites observed in summer (Figure 4). Higher GPP was evident in both the gap-filled totals (Table 3.3) and GPmax (Figure 3.2) calculated using non-gap-filled data. Light response parameters (Table 3.2) reveal higher GPP was associated with increased photosynthetic capacity, rather than photosynthetic efficiency, the latter which was similar to Kopuatai. The most likely explanation for this is the greater abundance of shrubs which has been shown to have higher GPmax compared to other components of peatland vegetation (Moore et al., 2002; Bubier et al., 2003; Peichl et al., 2018). Although we did not measure standing biomass or photosynthetically active leaf area, the greater abundance of shrubs at Moanatuatua is likely to have contributed to higher values of both. *E. robustum* and *E. pauciflora* occupy different parts of the canopy (de Lange et al., 1999) and the woody stems of *E. pauciflora* have been observed to support *E. robustum*, allowing it to occupy a space higher in the canopy.

3.5.3 Plant traits as a moderator of the response of GPP to water table

Water table position was a major control for GPP at Moanatuatua (Figure 6), limiting at both shallow and deep extremes, with this effect strong enough to be observed in the measured NEE flux (Figure 3.3). In contrast, at Kopuatai, WT was found to have little effect on GPP (Figure 3.6), as was previously found to be the case during the most extreme drought in 70 years (Goodrich et al., 2017). In order to explain the difference in the response of GPP to WT in these sites, and elsewhere in the literature, it is necessary to consider the processes which regulate WT in peatlands, and the sensitivity of peatland plants to WT variation. For peatlands in general, GPP has a theoretical optimal WT depth specific to the plant community present, above and below which GPP will be limited (Belyea and Clymo, 2001). Limitation of GPP under both wet and dry conditions is seldom observed in intact bogs, except in exceptionally dry years, due to the internal processes and feedbacks which maintain a shallow and stable WT optimal for plant growth (Fritz et al., 2008; Belyea, 2009; Kettridge et al., 2015). However, upon drainage this trait can be lost, and unstable, or fluctuating, WTs are a common feature of degraded bogs (Price et al., 2003). Typically, the WT regime becomes more extreme in degraded peatlands as the mean WT moves deeper into more degraded peat, and additionally, peat decay is accelerated, with loss of

porosity and a corresponding decrease in the specific yield (Ingram, 1978; Schouwenaars, 1993).

Early investigations into peatlands noted the importance of hydrology in determining plant distribution (e.g. Aiton, 1805; Boate, 1652), providing an early insight into the varying tolerance of different peatland species to wet and dry conditions, since confirmed by the modern scientific method (Rutter, 1955; Laitinen et al., 2008; Radu and Duval, 2018). As such, it is not surprising that many different responses of GPP to WT have been described in the peatland CO_2 flux literature. For example sometimes no response of GPP to WT fluctuation is observed (Gažovič et al., 2013), as we found for Kopuatai (Figure 3.6), sometimes GPP decreases with deep WTs (McVeigh et al., 2014; Strachan et al., 2016), other times it increases (Gatis et al., 2016) and occasionally parabolic responses are seen where GPP may be limited under both high and low WTs (Sonnentag et al., 2010; Euskirchen et al., 2014) as also observed here for Moanatuatua (Figure 3.6). Importantly, with the sustained lowering of WT the response of GPP to short term WT position is unlikely to remain static as the plant community usually changes over time as the ecosystem adapts to the new WT regime (Laine et al., 1995).

At Moanatuatua, the WT is not only deep, but also seasonal variation was extreme (maximum annual range of 704 mm), with 'extreme' having been previously defined as greater than 380 mm in Northern Hemisphere peatlands (Laitinen et al., 2008). Extreme fluctuation of the WT is usually associated with pronounced modification of, and even the loss of the peat-forming vegetation community (Price et al., 2003; Tuittila et al., 2004; Laitinen et al., 2008; Talbot et al., 2010), for example, in continental climates, a shift towards forest species can occur (Talbot et al., 2010), or in oceanic climates a shift towards species such as *Molinia caerulea* can be seen (Taylor et al., 2001), in both cases a shift to species which are relatively poor peatformers occurs (Gogo et al., 2011). Moanatuatua is unusual in that the peat-forming community remains intact, with major peatformers still dominant, and GPP remains high, albeit constrained by either extreme of WT fluctuation. Differing traits and tolerance to wet and dry conditions across plant species provide the most plausible explanation for both the persistence of the peat forming community at Moanatuatua and the differing response of GPP to WT at both sites.

The two peat-forming species, *E. robustum* and *S. ferrugineus*, are tolerant of a wide range of WT conditions (de Lange et al., 1999; Linder and Rudall, 2005; Hodges and Rapson, 2010). Plants within the *Restionaceae* family are characterised by an evolutionary history of adaptation to a combination of nutrient-poor conditions and seasonal drought (Linder and Rudall, 2005). In turn *Empodisma* and *Sporadanthus* genera are associated with a tolerance of seasonal inundation, rather than saturated conditions per-se and can equally often be found growing in sandy soils as well as peats (Pate and Meney, 1999). Both *E. robustum* and *S. ferrugineus* have well-developed aerenchyma (Campbell, 1964) which allow the plants to tolerate saturated conditions, permitting the survival of deep anchoring roots, down to one metre or more (Clarkson et al., 2009). These deeper roots can allow access to water, even in the late summer (Clarkson et al., 2009). Additionally, the metabolically important cluster roots of *E. robustum* also have the ability to form floating mats above the WT (Fritz et al., 2008), as observed at Kopuatai (data not shown). By keeping these roots above the WT the stress of anoxia may be avoided when WT is high. The combination of traits such as these cause *E. robustum* and *S. ferrugineus* to be physiologically well suited to a fluctuating WT. The persistence of the peat former *E. robustum*, in the face of low and fluctuating WTs, makes the eventual recovery of the ecosystem WT at Moanatuatua more likely because of its demonstrated conservative evaporation regime (Campbell and Williamson, 1997). However, the competitive displacement of *E. robustum* by faster-growing, higher nutrient demanding species (Meney et al., 1999) remains a strong threat to the ecosystem. Nutrient levels (nitrogen and phosphorus) and peat decomposition have increased at Moanatuatua since 1997 (unpublished data), likely as a result of the combined effect of lowered WT and fertiliser aerial drift from adjacent farmland.

In contrast to restiad peatformers, ericoid shrubs such as *E. pauciflora* are poorly adapted to extremes in WT, and thus are probably responsible for declining GPP at either WT extreme. For example in a South African heathland, ericoid shrubs were found to be more susceptible to drought than restiad species (West et al., 2012). Similarly, ericoid shrubs in some peatlands have been found to have reduced productivity at either extreme of WT fluctuation (Lafleur et al., 2003; Peichl et al., 2018). This lack of tolerance for WT extremes is reflected in the distribution of ericoid shrubs which are common in peatlands where WT is low, but are rare when WT fluctuation is extreme (Rutter, 1955; Laitinen et al., 2008).

Ericoid shrubs tend to be shallow rooted, due to an inability to transport oxygen to roots, owing to lack of aerenchyma (Shaw et al., 1990). Instead, they must avoid prolonged anoxia by limiting root growth to aerobic areas above the WT (Shaw et al., 1990). With the effect that the root system is largely ephemeral becoming inactive during high WT conditions (Read, 1996). Prior to WT lowering, *E. pauciflora* at Moanatuatua was recorded as having roots no deeper than 80 mm, and close to the approximate WT at the time (Campbell, 1964). However the *E. pauciflora* roots now extend deeper with the subsequent lowering of the WT (unpublished data). The rooting system of *E. pauciflora* now faces a compromise between avoiding anoxia in winter and maintaining access to water in late summer and autumn. It is therefore reasonable to suppose that the reduction in GPP at either extreme of WT fluctuation seen at Moanatuatua is primarily due to declining productivity of *E. pauciflora*, which, in contrast to the restiad species, is physiologically ill-suited to extreme WT fluctuation.

3.5.4 Ecosystem Respiration

Annual ecosystem respiration was on average 551 g C $year^{-1}$ (87%) higher at Moanatuatua than at Kopuatai and was greater for all months of the year (Figure 3.5), especially during the summer and early-autumn. It should also be noted that a portion of the difference may be due to higher GPP. This is because an estimated 50% of peatland ER is autotrophic in origin (Moore et al., 2002), with C fixed by photosynthesis persisting for only a short time within the ecosystem after uptake (Walker et al., 2016). Therefore ER would be expected to be greater in peatlands with a higher GPP, regardless of the rate of heterotrophic decay. Using the 50% estimate (Moore et al., 2002), greater GPP can explain less than 40% of the higher ER seen at Moanatuatua and this is unlikely to be the primary reason for higher ER. On a per-volume basis, surface peat at Moanatuatua has a lower rate of respiration than that of Kopuatai (18% less than Kopuatai in Hodge, 2002), therefore it is reasonable to assume that higher ER at Moanatuatua is primarily due to heterotrophic decay and the greater volume of peat exposed to oxidative decay above the WT as commonly assumed.

At Kopuatai ER appeared to change from temperature controlled to WT controlled, once WT decreased below 100 mm, as indicated by the greater number of vertical rather than horizontal contours crossed in Figure 3.7, with the deeper WT correlating with higher ER. In contrast, at Moanatuatua, WT fluctuation appeared

to have very little, if any, impact on ER (Figure 3.7) in agreement with findings of Campbell et al. (Campbell et al., 2014). Inclusion of WT as a variable in the gap-filling ANN for Moanatuatua did not improve the performance of the gap-filling model, lending further credence to the idea of instantaneous movement of WT having little net effect on ER. The different response of ER to WT change seen at both sites can be best explained by the range of WT fluctuation each site experiences, as well as the history of the sites.

Carbon dioxide loss in peatlands upon water table lowering is not linear with time and the largest losses are usually seen upon initial lowering of the WT (Hargreaves et al., 2003; Laiho, 2006; Straková et al., 2012). This occurs because the surface peat in wet bogs is generally enriched in labile organic carbon which may readily decompose in response to oxygenation (Laiho, 2006). The potential for high ER to occur upon lowering of the WT at Kopuatai is clear, since the highest rates of ER occurring under dry conditions (Figure 3.7) in contrast to Moanatuatua. At Kopuatai the surface peat is typically saturated for much of the year (Campbell et al., 2002) and fluctuation of the WT below a certain threshold is likely to alter the oxygenation of the surface peat, which is enriched in labile carbon (Kuder et al., 1998). In contrast, at Moanatuatua, movement of the WT instead affects the saturation of sub-surface peat (deeper than 10 cm), which is highly depleted in labile carbon (Kuder et al., 1998) and has been found to be more resistant to decay than peat from the same depth at Kopuatai (Smith, 2003). At Moanatuatua even when the WT was highest in early spring, the moisture content of the surface peat remains extremely low (approx. 20% water by volume in Campbell et al. 2002), well below the threshold found to permit aerobic respiration (60% in Husen *et al.*, 2014).

3.6 Conclusion

Our data support the idea that long-term water table position can cause peatland CO_2 fluxes to respond differently to environmental drivers such as light and instantaneous movement of the water table. At Moanatuatua (drainage-affected) higher photosynthetic capacity and gross ecosystem productivity were observed than at Kopuatai (hydrologically pristine), most likely as a result of greater ericoid shrub cover. Higher gross primary productivity in turn mostly offsets greater ecosystem respiration, allowing Moanatuatua to remain a sink for CO_2 and

demonstrating the resilience of the peatland CO_2 sink to water table lowering across the timescales observed.

The restiad peatland CO_2 sink appears to be more resilient to a low water table than that of other peatland types, due to the wide range of water table conditions that the main peatformer *E. robustum* is able to tolerate, in contrast to *Sphagnum* mosses, and some sedges, which are known to have a narrower range of tolerance. The hydrological properties of the peat, and thus water table fluctuation, are expected to continue to change in response to ongoing decay and the lowering of the mean water table depth. If this occurs, tolerance of both deep and fluctuating water tables, will become an ever more important plant trait, one which is well expressed in the main peatformer *E. robustum*, but not in the ericoid shrub *E. pauciflora.* Water table fluctuation is already limiting gross primary productivity at Moanatuatua and may well cause the bog to become a net source of CO_2 in the future. Additionally, we expect Moanatuatua to be more vulnerable to CO_2 loss during periods of hydroclimatic extremes, such as droughts. The persistence of the peat former *E. robustum*, in the face of low and fluctuating water tables, makes the eventual recovery of the ecosystem more likely. Despite this competitive displacement of *E. robustum*, with more nutrient-demanding species remains a strong threat.

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Chapter Four

Recovery of the CO_2 sink in a remnant peatland following water table lowering

4.1 Abstract

Peatland biological, physical and chemical properties change over time in response to alterations in long-term water table position. Such changes complicate our ability to predict the response of peatland carbon stocks to sustained drying. In order to better understand what effect sustained lowering of the water table will have on peatland carbon dynamics, we re-visited a drainage-affected bog, repeating eddy covariance measurements of CO_2 flux after a 16-year interval. We found the ecosystem CO_2 sink to have strengthened across the intervening period, despite a deep and fluctuating water table. This was mostly due to an increase in CO_2 uptake through photosynthesis associated with increased shrub growth. We also observed a decline in CO_2 loss through ecosystem respiration. These changes could not be attributed to environmental conditions. Air temperature was the only significant contemporaneous driver of monthly anomalies in CO_2 fluxes, with higher temperatures decreasing the net CO_2 sink via increased ecosystem respiration. However, the effect of air temperature was weak in comparison to the underlying differences between time periods. Therefore, we demonstrate that for drying peatlands, long-term changes within the ecosystem can be of primary importance as drivers of CO_2 exchange. In this peatland, the ecosystem carbon sink has shown resilience to water table drawdown, with internal feedbacks leading to a recovery of the CO_2 sink after a 16-year interval.

4.2 Introduction

Peatlands store in excess of 600 GT of carbon (C) (Dargie et al., 2017; Page et al., 2011; Yu, 2011), comparable to the total amount emitted by anthropogenic sources since the industrial revolution (~ 500 GT C in Allen et al., 2009). Hydrology plays a prominent role in peat formation with a shallow and stable water table maintaining anoxic conditions and suppressing microbial decay of dead plant matter. Globally, major areas of peatland are experiencing drying as a result of recent climate change (Long et al., 2017; Zeng et al., 2014) and this trend

is expected to continue (Wu et al., 2015). There is concern that drying peatlands could act as a positive feedback on the global carbon cycle through release of stored C as CO_2 (Dise and Phoenix, 2011; Straková et al., 2012). The response of peatland carbon and water dynamics to environmental variables is tightly regulated by complex internal processes and feedbacks, which operate over varying timescales (Belyea, 2009; Belyea and Baird, 2006; Waddington et al., 2015), potentially over periods of centuries or more (Swindles et al., 2012). The feedbacks inherent in peatlands make their response to drying difficult to predict beyond a few years, and are likely to lead to substantial under- or overestimates of peatland response to global climate change (Dise, 2009).

Much of the current understanding of how peatlands respond to external drivers beyond the sub-decadal scale comes from palaeoecology (e.g. Swindles et al., 2017; Yu, 2011). However, achieving a high resolution, or sub-centennial, record is challenging, and uncertainty about past environmental conditions is often high. The decadal to centennial time scale is arguably the most important, in the context of global climate change, as evidenced by the widely accepted use of the 100-year and 20-year timeframes for reporting greenhouse gas emissions as CO_2 equivalents, yet this timescale is the most poorly understood, falling outside of most contemporary studies and at a resolution that is difficult to capture using a palaeoecological approach (Frolking et al., 2014; Ratcliffe et al., 2018).

A growing number of eddy covariance (EC) records exist for peatlands, but very few span more than a few years. Long-term EC measurements have the potential to complement existing understanding of long-term climatic response of peatland C. They provide high temporal resolution and well confined data on CO_2 exchange and environmental drivers beyond annual timescales, allowing better mechanistic understanding of feedbacks occurring within peatlands. Long-term records have also provided unexpected insights, for example that the summer CO_2 uptake is dependent on the previous winter mean temperature, demonstrating that the effects of meteorological drivers on C fluxes can be asynchronous (Helfter et al., 2015; Peichl et al., 2014). The opportunities for studying long-term change substantially increase if sites where EC measurements were previously undertaken are recommissioned, offering a valuable opportunity for studying long-term changes in ecosystems. Measurements spanning long time periods are particularly important for peatlands which have undergone water table lowering, as the drivers

of C exchange are known to be temporally variable (Mäkiranta et al., 2009; Straková et al., 2012). Changes in the long-term water table position cause a large number of competing processes and feedbacks to become active (Laiho, 2006; Swindles et al., 2012; Waddington et al., 2015), yet the timing and the relative strength of these is poorly understood, as are the net effects on CO_2 emissions.

One of the key processes which can lead to the stabilisation, or recovery, of the carbon sink following water table lowering is the "water table depth peat decomposition" negative feedback (Waddington et al., 2015) where changes in peat physical (Holden et al., 2004) and chemical (Fenner et al., 2005) properties limit further decay and promote the recovery of a near-surface water table. Another key process is an increase in primary productivity (Laiho, 2006) where more nutrient demanding plants with greater photosynthetic capacity tend to increase in dominance after water table lowering (Laiho, 2006).

While both of these processes are important for restoring the C sink, a number of competing positive feedbacks can also contribute to an increase in the loss of C. For instance, the "water table depth specific yield feedback", by reducing the capacity of the peat to hold water, can result in an unstable water table (Waddington et al., 2015) reducing CO_2 uptake (Ratcliffe et al., 2019). Similarly, an increase in plant productivity can result in concurrent increases in the degradability of the plant matter and this is often seen in degraded peatlands (Bauer, 2004; Gatis et al., 2016). However, the net effect of shrub expansion, the "shrubification" feedback, is still uncertain (Waddington et al., 2015). The paleoecological record also reveals a heterogeneity of long-term responses, peatlands may sometimes be resilient to drying, while other times there may be large hiatuses in C accumulation (Swindles et al., 2017). Ultimately, the autogenic hydrological feedbacks that make peatlands resistant to seasonal water deficit are only efficient within a certain range of environmental conditions and peatlands will not be resilient beyond a certain threshold of drying (Alexandrov et al., 2016).

In order to better understand how drainage affects the peatland CO_2 flux over longer timescales we compare new EC measurements of CO2 flux with those carried out almost two decades earlier in a peatland which has now undergone at least a quarter of a century of lowered water table and for which the water table regime shows no sign of recovery. The site has also undergone nitrogen (N) and

phosphorus (P) enrichment, which are elevated compared to nearby bogs, and there has been an expansion of ericoid shrubs (Ratcliffe et al., 2019).

Our specific objectives are to compare CO_2 flux and its drivers between 1999-2000 and 2016-2017 in order to investigate long-term trends in C dynamics for peatlands undergoing drying, and associated nutrient enrichment and expansion of shrub cover.

4.3 Study site and method

4.3.1 Study site

Moanatuatua (37.92515° S, 175.36967° E, altitude 65 m) is a remnant of a lowland raised bog situated in Te Ika-a-Māui (North Island) of Aotearoa New Zealand. The climate is fully humid, meaning it lacks a strong seasonal trend for precipitation, and sits within the warm temperate climatic zone, with warm summers, i.e. Cfb, as defined in the updated Köppen Geiger climate classification (Kottek et al., 2006). The 30 year (1981-2010) mean annual temperature is 13.6 °C with annual rainfall of 1202 mm (NIWA, 2017). The peatland is classed as restiad (dominated by Restionaceae) with *Empodisma robustum* presently comprising 54.4% ± 7.1% cover, followed by the ericaceous shrub *Epacris pauciflora* (13.8 ± 4.3%) and Sporadanthus ferrugineus (6.6 ± 6.7%). Maximum vegetation height was 2.56 ± 0.12 m (Ratcliffe et al., 2019), comparable to a height of 2.3 m in 1993, but taller than in 1974 when it was recorded as 1.8 m (de Lange et al., 1999) all reported as mean ± 1 σ. The peat at the site is deep, varying between 7 and 11 m (Davoren, 1978). Prior to European colonisation of the Waikato region (circa. 1860), Moanatuatua was ~7500 ha in size (Clarkson et al., 2004). Drainage and conversion to pasture began in earnest in the 1930s and by 1949 half of the peatland had undergone conversion to agricultural land (Thompson and Elliott, 1952). By 1979 the bog was its present size with only 140 ha remaining with peat-forming vegetation and < 2% of the original extent (Matheson, 1979). Measurements of surface moisture content from 1967-1968 showed the surface peat at Moanatuatua to be saturated year-round (Luxton, 1982), while monthly water table measurements carried out in the remnant peatland in 1976 and 1977 shows a water table close to the surface varying between 80 mm and 380 mm below the peat surface (Matheson, 1979). Both datasets are consistent with earlier anecdotal observations of a near-surface water table

(Cranwell, 1953, 1939). However, recent measurements repeated since 1995 suggest a large decline in water table depth relative to 1977, e.g. a summer low of 600 mm in 1994 (Sharp, 1995), 650 mm in 1995 (Clarkson et al., 1999) and 813 mm in 2000 (Campbell et al., 2014). There are no accounts of the water table being above the surface. Pre-drainage investigations showed relatively un-decomposed peat at the surface of Moanatuatua which was enriched in carbohydrates (Bailey, 1953), commonly accepted as indicating a lack of decay (Leifeld et al., 2012), while by the late 1990s this was no longer the case (Kuder et al., 1998). The site has been undergoing nutrient enrichment; with higher N and P in the surface peat relative to pristine peat bogs (Clarkson et al., 2004) and this has become more pronounced in recent years (Table 1).

Table 4.1. Supporting information on nutrients (% mass) in the surface peat at Moanatuatua, spanning the period of high and stable water table depth (pre-1976), moderately low and fluctuating water table (1994-1996) and deep and highly fluctuating (1997 until present).

Reference	Year	C%	N%	P%	C:N
Luxton (1982)	1967-1968	46-47	0.63-0.69	-	73 - 68
Thompson (1997)	1995	-	0.96	0.03	-
Clarkson (1999)	1997	-	0.86	0.03 (n=6)	-
Clarkson Unpublished	2018	55.3 (n=8)	1.6 (n=8)	0.04 (n=8)	35 (n=8)

4.3.2 CO_2 flux and ancillary measurements

Eddy covariance measurements of CO_2 flux were made over two periods, close to the centre of the present-day bog, the first from 01/01/1999 to 24/12/2000 is referred to as the early period. The results of the early period were first published by Campbell et al. (2014). In 2015, EC measurements resumed with a new site established within 20 m of the original site. Some of this later data period was reported in Ratcliffe et al. (2019), however, for the sake of seasonal comparability for the current study we analysed a different, but overlapping, period from 01/01/2016 until 31/12/2017, referred to as the recent period. The key variables measured and the instruments used are summarised in Table 1. Further details on instrumental setup are available in Campbell et al. (2014) and Ratcliffe et al. (2019) for the early and recent periods, respectively.

Table 4.2. Key measurements and sensors used in the two different study periods including ancillary data

	1999-2000	2016-2017
Sonic anemometer 3D wind	CSAT3 Campbell Scientific Inc., USA 10 Hz	CSAT3, Campbell Scientific Inc., USA 10 Hz
Infrared gas analyser CO_2, H_2O	LI-6262, LI-COR, USA (closed path) 10 Hz	LI-7500, LI-COR, USA (open path) 10 Hz
Photosynthetic photon flux density	LI-190SZ, LI-COR, USA	BF5, Delta-T, UK
Rainfall	TB3, Hydrological Services, Australia	TR-525M, Texas Electronics, USA
Water table depth	Capacitance probe (model 392), Dataflow Systems Pty. Ltd., New Zealand	WL1000W, Hydrological Services, Australia
Air temperature and humidity	HMP-35C, Vaisala Inc., Finland	HMP 155, Vaisala Inc., Finland

4.3.3 Flux data processing and quality control

Where possible, flux processing was standardised for both datasets. Original 10 Hz data from 1999 and 2000 were re-processed in line with current best practice. For the early data, the raw CO_2 concentrations, stored as millivolt signals, were post-processed using zero and span gas calibration signals embedded in the original time series at 12:30 am every night. For both measurement periods, half-hourly CO_2 and H_2O fluxes were calculated from high-frequency data using the EC software EddyPro™ 6.2.0 (LI-COR Inc., USA). The effects of air density fluctuations for the open path measurements in the recent dataset were compensated according to Webb et al. (1980). Fluxes associated with low friction velocities, below 0.09 ms-1 were rejected following the u* threshold detection method described by Reichstein et al. (2005). The semi-analytical technique of Fratini et al. (2012) was used to correct for spectral loss and was used in preference to other methods as it was more appropriate for closed path systems, but applicable to open path systems as well. Both datasets were subjected to the same statistical filters proposed by Vickers and Mahrt (1997) and implemented in EddyPro™. This included filtering for spikes, amplitude resolution, dropouts,

absolute limits and kurtosis. Data were flagged using the quality parameters described by Mauder & Foken (2004) and 'bad' Flag 2 data were discarded. 'Good', Flag 0, and 'moderate', Flag 1, date were used for monthly and annual flux totals while only Flag 0 data, were used in the temperature and light response analyses. A 40-day moving window filter was then applied to the data to remove soft spikes (Campbell et al., 2014). Values which exceeded 2.9 times the standard deviation, chosen from visual inspection, for either night time or day time data were flagged. Any point flagged more than twice as the window moved was then removed. After all filtering steps a total of 38% data remained for the early period and 43% for the recent.

Gaps in the data were filled using an artificial neural network (ANN) (Papale and Valentini, 2003), following Ratcliffe et al. (2019). Two models were used, one for daytime conditions, the other for night-time. Both models used fuzzy variables for season (Papale and Valentini, 2003) and shared inputs of air temperature, phytomass index (following Aurela et al. 2001) and water table depth. The daytime models had an additional inputs of photosynthetic photon flux density (PPFD) and vapour pressure deficit. Both models were found to perform similarly well with a combined day night $R_2 = 0.83$ for the early period and $R_2 = 0.77$ for the recent period.

4.3.4 Flux terminology and partitioning

We adopted the CO_2 flux terminology recommended by Chapin et al. (2006). Net ecosystem production (NEP) is used for monthly and annual flux totals (units g C m^{-2} $period^{-1}$) and is the net result of two processes, uptake of CO_2 from the atmosphere via gross primary production (GPP) and release to the atmosphere via ecosystem respiration (ER). For NEP, positive values indicate an ecosystem CO2 sink while negative values a CO_2 source. GPP and ER are always positive. Net ecosystem exchange (NEE) is used for 30-minute data (units μmol CO_2 m^{-2} s^{-1}) and uses the opposite sign convention to NEP. We partitioned measured NEE by assuming night-time NEE (night-time defined as PPFD < 20 μmol m^{-2} s-1) to be equivalent to ER, i.e. NEE=ER with GPP set to zero. Daytime ER was then modelled by applying the night-time ANN to daytime drivers (Oikawa et al., 2017; Ratcliffe et al., 2019). GPP was then recalculated as NEE–ER. This method is known to perform equally well as other standard approaches, for instance that of Reichstein et al. (2005), but may overestimate ER and GPP by 10-13% (Oikawa

et al., 2017), because ER tends to be lower than previously thought during the daytime (Keenan et al., 2019; Nielsen et al., 2018). Non-standard approaches to estimating GPP, such as isotope partitioning (Oikawa et al., 2017), or carbonyl sulphide derived GPP (Asaf et al., 2013) remain technically challenging and thus were not used. We are therefore cautious in interpreting the absolute values of GPP and ER, but consider relative comparisons between time periods to be valid.

4.3.5 Uncertainty analysis

Uncertainty analysis for NEP was carried out following the procedure of Elbers et al. (2011). Estimates of uncertainty included the effect of selection of the u* threshold χa; statistical screening χb; measurement error χc; and flux calculation uncertainty χd, with each term incorporating the effect of uncertainties in the ANN gap filling model. In order to calculate χa we altered the u* threshold ± 0.05 m s-1 (i.e. 0.04 and 0.14), χb was calculated by altering the thresholds on the moving window filter by 0.5 stdev (i.e. 2.4 and 3.4 stdev) while χc and χd were calculated following the successive days method of Dragoni et al. (2007). Measurement error in the early data (χc 8.3 g C m-2 year-1) was more than twice that for the recent data (χc = 3.0 g C m-2 year-1), likely reflecting improvements in instrumental precision, however, the largest source of uncertainty was χa, which tended to be greater in 1999/2000, with the total NEP being highly sensitive to a reduction in the u* threshold, and is the main reason for the higher uncertainty in the earlier time period, whereas χb, χc and χd were comparable between periods. The final reported uncertainties, χt, were calculated as:

Equation 1

$$\chi t = \sqrt{\chi^2 a + \chi^2 b + \chi^2 c + \chi^2 d}$$

4.3.6 Environmental data

A weather station at Hamilton airport, less than 8 km from the study site, was used to provide 30-year normals for precipitation and air temperature (NIWA, 2017). To account for known differences in instrument sensitivity for PPFD, datasets were adjusted to match values at a weather station (~65 km from the site) which had continuous measurements of incoming solar radiation spanning both periods. This was done by regressing contemporaneous measurements of incoming solar radiation at mid-day under clear sky conditions for both the early

instrument (R_2=0.93) and the recent instrument (R_2=0.99). The light response of NEE is indicative of fundamental photosynthetic properties (Ögren and Evans, 1993) and therefore the seasonal light response of NEE was described using the Michaelis-Menten rectangular hyperbolic function derived from 30-min observed data. This timescale was chosen as it captures the near-instantaneous response of the ecosystem to light, and relies only on measured rather than modelled fluxes and thus is more suitable for assessing a fundamental aspect of ecosystem functioning.

Equation 2

$$NEE = \frac{\alpha . PPFD . GPmax}{\alpha . PPFD + GPmax} + ER_0$$

Where α is the initial slope of the light response curve at low light (photosynthetic efficiency); GPmax is photosynthetic capacity; and ER0 is ecosystem respiration at PPFD = 0 µmol m^{-2} s^{-1}. Statistical analysis

To investigate the effect of air temperature, PPFD and water table on ER, gap filled data were converted to monthly values (means or totals) and standardised by subtracting the value for each month from the mean value for that month for the four years of data. Measurement period was defined numerically as 0 for the early period and 1 for the late. Pearson's rank correlation was then calculated on the standardised monthly data (Table 4) to assess the relative strength of correlation between potential drivers and anomalies in CO_2 fluxes. Monthly timescales were chosen to compensate for seasonal trends, for example comparing each month with the same month in different years.

4.4 Results

4.4.1 Weather and climate

The years 1999, 2016 and 2017 were all warmer than the long term air temperature (1981-2010) average, 13.6 °C, with annual mean temperatures of 14.3, 14.4 and 14.9 °C respectively. In contrast, 2000 was cooler than the long-term average, at 13.4 °C. Both 2016 and 2017 were also exceptionally warm when the intervening years in between measurements periods are considered (Supplementary Figure 1) The first two measurement years, 1999 and 2000, were relatively dry with rainfall totalling 1066 mm and 815 mm respectively, well

below the annual normal (1981-2010) of 1227 (adjusted from: NIWA, 2017 to account for minor localisted differences). In contrast, rainfall in 2016 was near-normal with 1248 mm and 2017 was wet with 1462 mm (Figure 1b), with most of the excess rainfall occurring during late summer and autumn, while rainfall in 2017 was high, it was not exceptional compared to some of the intervening years, such as 2004 and 2011 (Supplementary Figure 1). Variation in rainfall was broadly reflected in annual water table regimes. The water table regime for 2017 was strikingly different from other years (Figure 1c), so much so that the water table was on average 226 mm higher than the four-year average across the autumn and winter from March to September. Towards the end of 2017, the water table returned to a position typical of the other measurement years as precipitation returned to normal (Figure 1). In contrast, the water table in autumn 2016 was notably deeper than the same time period in 1999 and 2000, despite similar cumulative precipitation to that time.

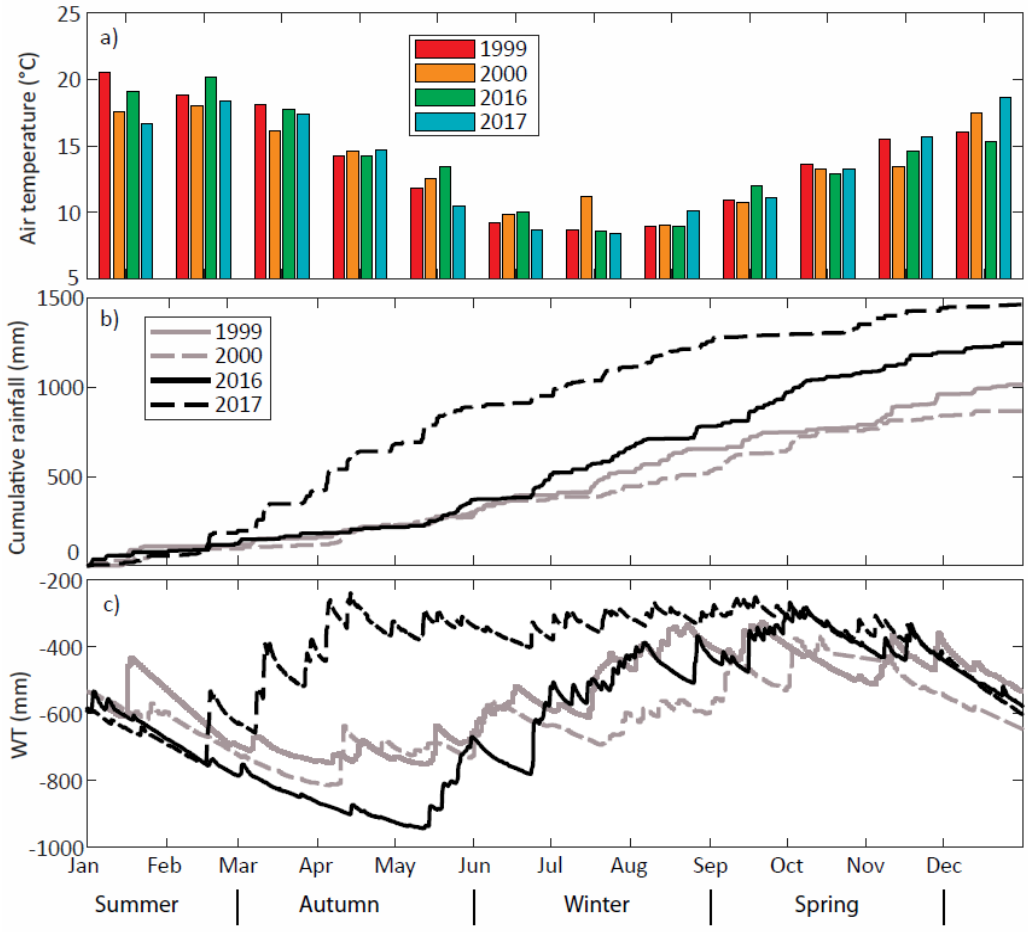

Figure 4.1. (a) Mean monthly air temperature (b) cumulative rainfall (c) water table depth relative to the peat surface at Moanatuatua bog for the four study years. Seasons were defined as Spring:

September to November, Summer: December to February, Autumn: March to May and Winter: June to August.

4.4.2 NEE and CO_2 flux components

The seasonal diurnal pattern of NEE was examined in the form of ensembles where the mean half-hour values were plotted for each year using filtered, non-gap filled data. The diurnal pattern of NEE shifted between study periods, most notably through greater net uptake of CO2 during the middle of the day during spring, summer and autumn (Supplementary Figure 2). For all daytime data NEE was on average -1.4 µmol m^{-2} s^{-1} different, i.e. there was grew (Figure 2), indicating greater uptake by photosynthesis in the recent period. Night-time CO2 loss through ecosystem respiration was also on average 0.43 µmol m^{-2} s^{-1} lower in the more recent period (Figure 2). While this is more conservative than the difference in daytime uptake, applied to all night and day half-hours it scales to 159 g C m^{-2} yr^{-1} and thus is considerable.

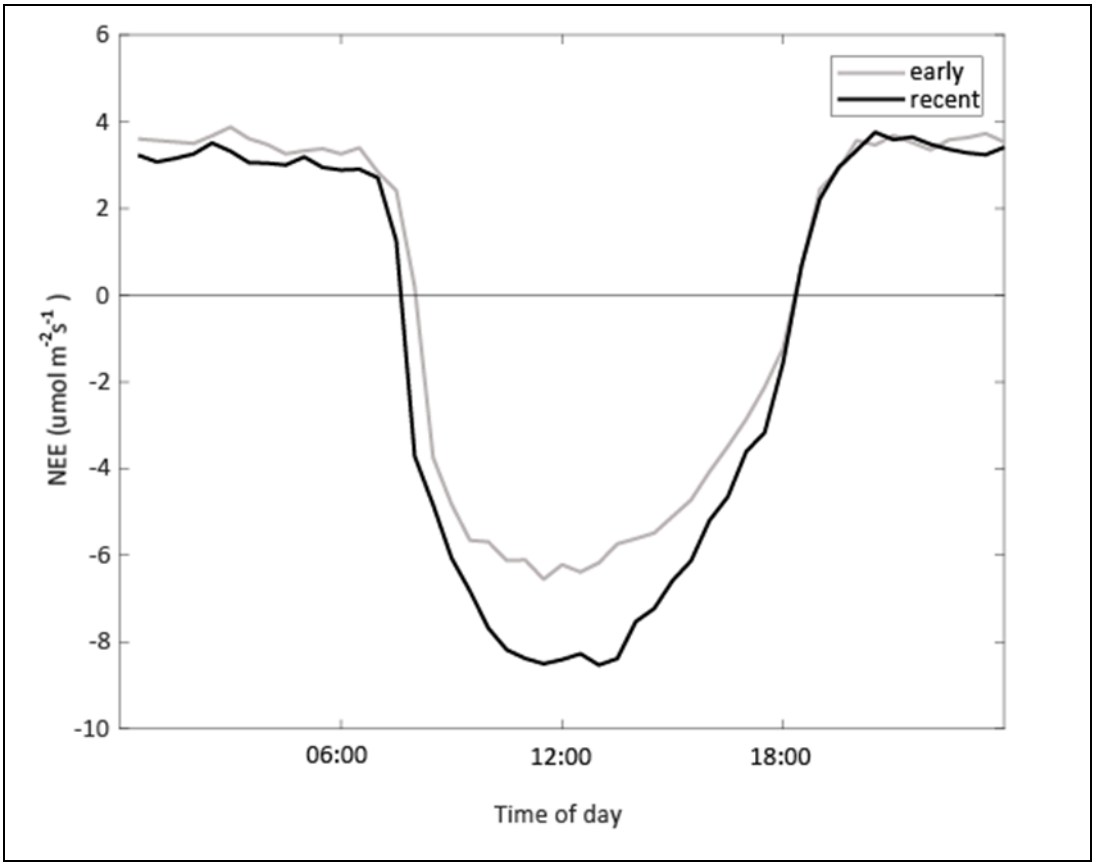

Figure 4.2. Yearly ensembles of filtered NEE (non-gap filled) split into Spring, Summer Autumn and Winter

Cumulative annual NEP (Figure 3) revealed differing patterns of CO_2 uptake between the two time periods, but also considerable within-period variation. For

the recent period, 2016 and 2017 displayed both greater net uptake during summer and smaller losses during winter compared to the earlier period, with the CO_2 sink recovering earlier in the year, around October in the recent period compared to November in the earlier period. The first half of 2017 was somewhat exceptional compared to the other years, accumulating nearly twice as much CO_2 compared to the same time period in 2016 and 2000 and maintaining a near neutral NEP in the autumn and early winter. The mid- to late-summer of 1999 also stands out as little to no net CO_2 accumulation occurred.

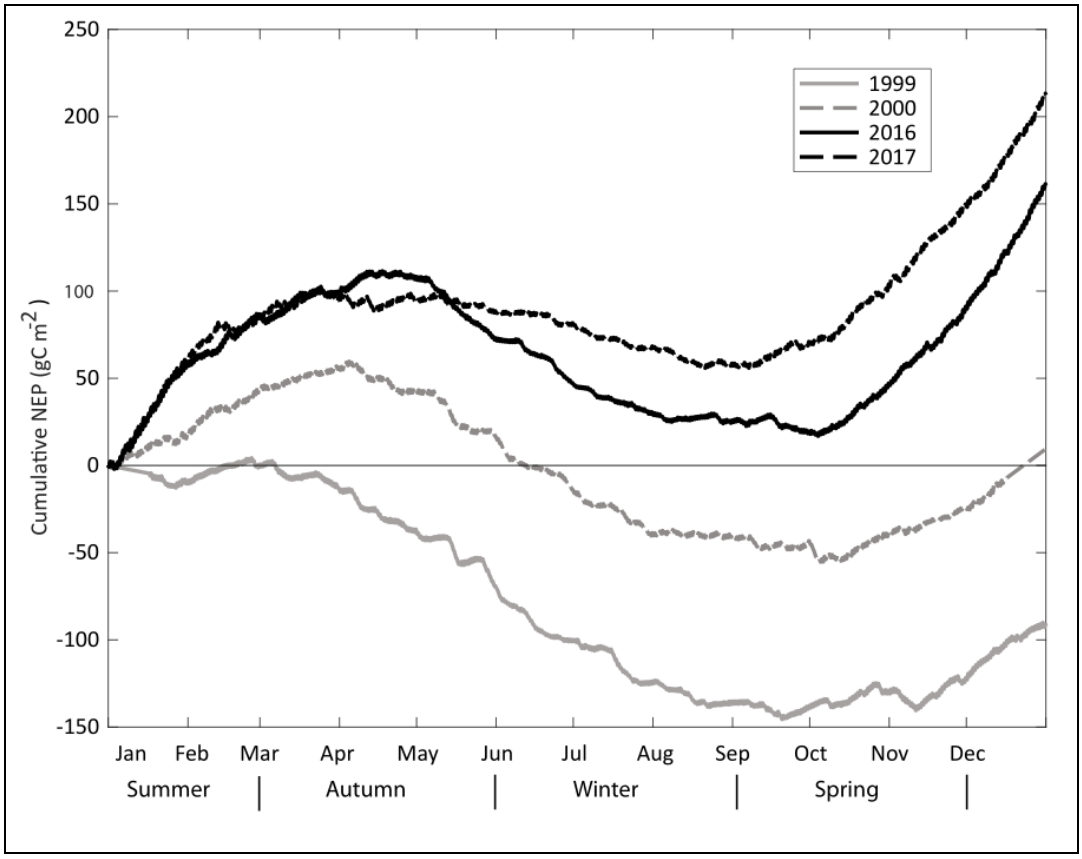

Figure 4.3. Cumulative NEP for the four measurement years

Component CO_2 fluxes GPP and ER were plotted for each measurement year (Figure 4). GPP was consistent through the autumn and winter but varied most inter-annually in the spring and the summer, with lower values in 1999 and 2000. Ecosystem respiration was more variable and clear differences between periods were most apparent over the winter period. The annual difference in gap-filled ER, 69 g C m^{-2} yr^{-1}, (Table 3) was smaller, but still comparable, to the difference implied by ensembles of the filtered data (Figure 2). Monthly NEP were consistently lower in 1999 and 2000 and this was most apparent during winter

when ER was higher in the early period, and in spring and summer when GPP was lower.

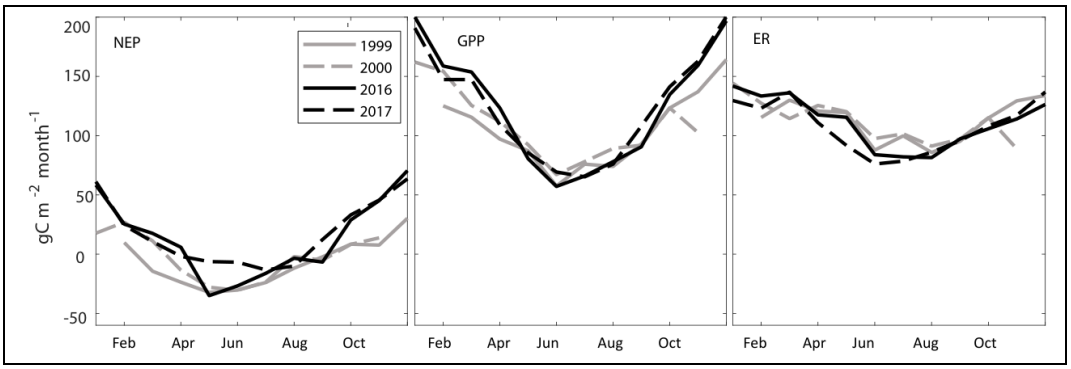

Figure 4.4. Total monthly NEP, GPP and ER for the four measurement years

Table 4.3. Annual flux totals and NEP uncertainties (gC m^{-2} yr^{-1}), mean annual air temperature (MAT, °C) and mean annual precipitation (MAP, mm $year^{-1}$) for each measurement year and averages for each period.

Year	NEP	GPP	ER	MAT	MAP
1999	-88 ± 35	1208	1368	14.3	1066
2000	-3.1 ± 34	1348	1344	13.4	815
2016	167 ± 16	1472	1307	14.4	1248
2017	209 ± 21	1475	1266	14.9	1462
Early period	-43	1314	1356	13.9	941
Late period	188	1474	1287	14.7	1355

4.4.3 Flux drivers

To better understand CO_2 flux drivers, we examined correlations with environmental anomalies and measurement period (Table 4). None of the environmental variables correlated significantly with anomalies in GPP, with PPFD ($p = 0.57$) being the closest to significance. The only significant correlating factor for GPP was measurement period ($p = < 0.01$). Variation in ER was also a significant driver of anomalies in NEP, with NEP also correlating significantly with air temperature, measurement period and water table depth. There was a weak correlation between measurement period and water table depth, meaning the two are interacting terms, and the water table was significantly shallower in the recent measurement period, likely due to the exceptional rainfall in 2017 (Figure 1). No such cross-correlation existed for air temperature. When the two time

periods were analysed separately, the effect of the water table was insignificant, and for the early (p = 0.27) and recent (p = 0.56) period.

Table 4.4. Pearson's rank correlation coefficients between standardised net ecosystem production (NEP), gross primary production (GPP), standardised ecosystem respiration (ER), water table depth (WTD), monthly air temperature (Ta) photosynthetic photon flux density (PPFD). Period refers to either the early (1999-2000) or the recent (2016-2017) measurement campaign, Significant values (p<0.05) are displayed in bold.

	NEP	GPP	ER	Ta	WTD	PPFD	Period
NEP	**1**	**0.81**	**-0.35**	**-0.33**	**-0.18**	0.05	**0.70**
GPP		1	0.26	-0.02	-0.05	-0.80	**0.50**
ER			1	**0.52**	**0.37**	-0.04	**-0.35**
Ta				1	0.22	-0.04	0.01
WTD					1	-0.16	**-0.3**
PPFD						1	0.22
Period							1

4.4.4 GPP and light response

To assess if there had been any changes in CO2 uptake between the two time periods the response of NEE to light was analysed. GPmax increased between measurement periods and light response curves of NEE revealed a greater response of NEE to high light levels, with a higher light saturation threshold in the more recent period as indicated by the slope of the line. Light response displayed a greater seasonality in the modern period, with GPmax varying by 9.5 μmol m−2 s−1 in the recent period compared to 1.9 μmol m−2 s−1 in the earlier period.

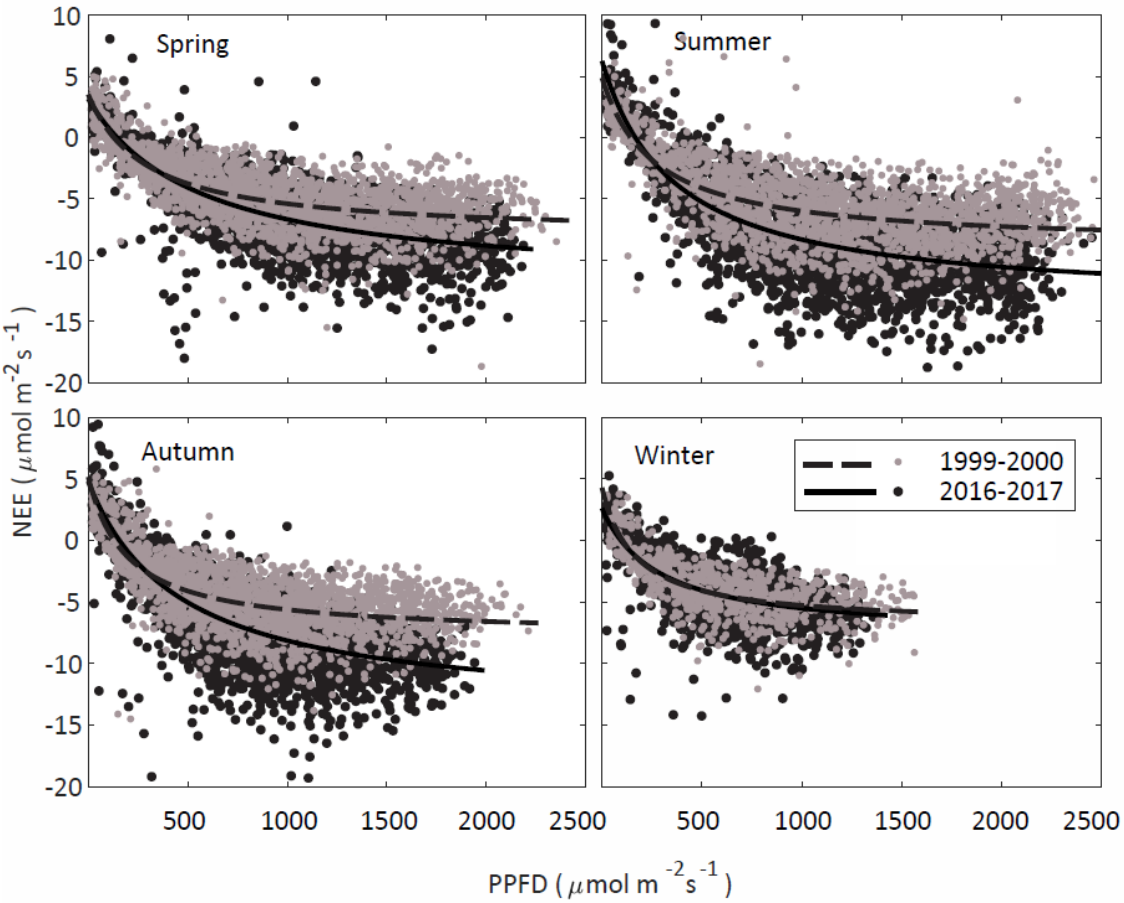

Figure 4.5. Light response of NEE for Moanatuatua bog for the two measurement periods. Curves were fitted using equation 2 to 30-minute NEE (points). Seasons were defined as the following: Spring: Sept.-Nov.; Summer: Dec.-Feb;. Autumn: Mar.-May; Winter: Jun.-Aug.

Table 4.5. Light response curve parameters from Moanatuatua. GP_{max} and ER_0 have units of μmol m^{-2} s^{-1} and α has units mol CO_2/mol photons

Parameter	Spring	Summer	Autumn	Winter	Annual
			Early (1999 – 2000)		
α	-0.040	-0.049	-0.066	-0.067	-0.056
GP_{max}	11.5	13.4	12.9	11.2	12.3
ER_0	3.5	4.5	5.2	4.3	4.4
			Recent (2016 – 2017)		
α	-0.027	-0.055	-0.041	-0.037	-0.040
GP_{max}	15.4	19.9	18.9	10.4	16.2
ER_0	3.2	6.3	4.8	2.6	4.2

4.4.5 ER and response to temperature

The effect of the measurement period and temperature anomalies on ER, monthly temperature and ER anomalies were plotted for each period. This displayed a downwards shift in ER irrespective of air temperature anomaly. For example,

when a month from 1999-2000 was cooler than the four-year air temperature mean, it more often than not resulted in ER being higher than the four-year ER average, rather than lower. Despite the recent period being warmer (on average the recent period was 0.8 °C warmer, Figure 1), ER was 69 g C m^{-2} yr^{-1} less.

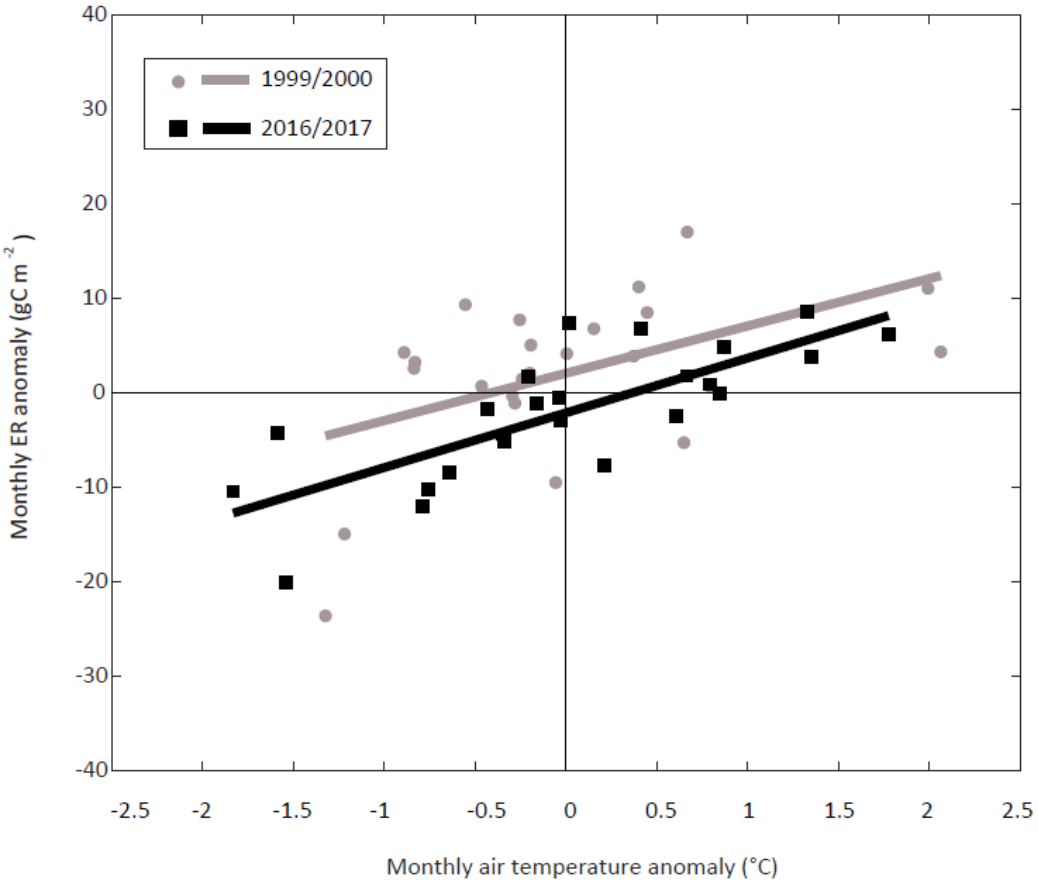

Figure 4.6. Air temperature anomalies and ER anomalies for each month of measurements. Anomalies are calculated from the monthly mean (air temperature) and total (ER) subtracted from the four year mean for that month. Lines represent linear regressions.

4.5 Discussion:

We found NEP to be much greater in the recent time period. During the early period the bog was a source for CO^2 (Figure 3., Table 3.) comparable to other disturbed peatlands (Waddington et al., 2002). In contrast, during the more recent two years the bog was a moderate to strong CO^2 sink (Figure 3, Table 3). The greater NEP in the recent period was primarily due to greater CO^2 uptake via GPP (Figure 4, Table 3) and to a slightly lesser extent, lower losses of CO^2 due to ER (Figure 4, Table 3). This was consistent with the difference implied from the filtered data (Figure 2), as well as the gap filled annual totals, where the difference in ER was 69 g C m^{-2} yr^{-1}(Table 3).

The values of NEP presented here for 1999 and 2000 were considerably lower than a previous estimate (234 C g m^{-2} yr^{-1} in Campbell et al., 2014 for the same time period) and reflects multiple changes in the data processing. Primarily, it was discovered that the LI-6262 water vapour dilution correction was not applied in Campbell et al. (2014) which is likely to have resulted in a overestimation of NEP, about 150 g C m^{-2} yr^{-1} (data not shown) and we attribute the remaining differences to other factors such as the use of standardised flux calculation software EddyPro, with the introduction of quality control flags (Mauder and Foken, 2004), standardised statistical tests (Vickers and Mahrt, 1997) and an updated spectral correction procedure (Fratini et al., 2012).

In contrast to the early period, NEP in the recent period was high for a bog at 188 g C m^{-2} yr^{-1} , closer to that of a treed fen (189 g C m^{-2} yr^{-1} Flanagan and Syed, 2011) than other bogs, the closest analogue being a blanket bog in Forsinard, Scotland (115 g C m^{-2} yr^{-1} Levy and Gray, 2015). The values are, however, comparable to an undrained restiad bog in the same region (204 g C m^{-2} yr^{-1} averaged from: Goodrich et al., 2017; Ratcliffe et al., 2019). The average annual NEP of 72 g C m^{-2} yr^{-1} averaged over all four measurment years is more typical of NEP from other bogs e.g. Forsinard, Scotland and other temperate peatlands (Petrescu et al., 2015).

4.5.1 Impact of vegetation changes on GPP

Our results show GPP to have increased between measurement periods, with greater GPP and GPmax across all seasons other than winter (Figure 5, Table 5), and a greater seasonality of GPmax in the recent period. An increase in photosynthetic capacity is often seen in drying peatlands as vegetation changes towards more nutrient-demanding species that favour drier conditions, such as ericoid shrubs (Bubier et al., 2003; Moore et al., 2002; Munir et al., 2015), and has been identified as one of the key ways the peatland carbon store may recover following water table lowering (Laiho, 2006). The ericoid shrub *Epacris pauciflora* has been increasing in cover and stature at Moanatuatua over the 16-year interval between measurements. In 1999 *E. pauciflora* was a minor, albeit thought to be rapidly expanding, part of the plant community (de Lange et al., 1999; Thompson, 1997) with low *E. pauciflora* abundance (e.g. less than 2% of the biomass in Thompson, 1997). Low *E. pauciflora* abundance contrasts with the 2016/2017 measurement period when *E. pauciflora* was the second most abundant

component of the vegetation community (13.8% cover in Ratcliffe et al., 2019). Additionally, Moanatuatua has been undergoing N enrichment (Table 1), likely as a consequence of peat decay and enhanced N deposition from surrounding dairy farming practices. There is, however, little evidence of peatland species being able to directly utilise N to increase photosynthesis (Bubier et al., 2011; Juutinen et al., 2010) but rather increased photosynthetic capacity may come about indirectly through changes in plant species composition (Frolking et al., 1998). The photosynthetic capacity of contemporary Moanatuatua was elevated compared to that of a nearby hydrologically pristine site at Kopuatai and displayed a greater seasonality of GPP (Ratcliffe et al., 2019). The Moanatuatua GPmax of 1999 and 2000 were midway between those of the recent period and Kopuatai bog (Goodrich, 2015; Ratcliffe et al., 2019), both in terms of overall GPmax and seasonal variation in light response of NEE. Considering the greater seasonality of GPmax in the recent period, and that GPmax during winter conditions was not different for the two time periods, it seems likely that the overall increase in GPP and GPmax can be attributed to a component of the vegetation community which is mostly dormant in winter. Ericoid shrubs commonly undergo root die-off, with the plant becoming inactive when water tables are high (Read, 1996) that may lead to greater seasonality of GPP compared to other major components of the vegetation community. However, this needs to be confirmed, for example by leaf level measurements of photosynthesis.

4.5.2 Decline in ER across time periods

Variability in monthly ER was also an important contributor to variation in the annual CO_2 balance, most notably during the winter months (Figure 4). The decline in ER across time periods occurred despite an increase in GPP, which is all the more remarkable as usually a substantial proportion, as much as 50% of carbon fixed during photosynthesis, is respired in the form of autotrophic respiration and thus has a very short residence time within the ecosystem (Moore et al., 2002; Walker et al., 2016). Therefore, increased autotrophic respiration could be expected to obscure a decline in heterotrophic respiration. During the winter when GPP was comparable across time periods, the difference in ER was most apparent (Figure 4). We hypothesise that the decline in ER has been caused by a decline in heterotrophic respiration, since an increase in GPP, all other factors being the same, would result in an increase in ER through greater

autotrophic respiration, due to the metabolic costs the enhanced productivity entails (Baldocchi and Penuelas, 2019). Therefore, heterotrophic respiration is highly likely to have declined between the two measurement periods.

A possible mechanism for a decline in heterotrophic respiration is peat organic matter quality. It is well known that lowering of the peatland water table results in a decline in organic matter quality of existing peat with the loss of labile organic matter (Könönen et al., 2016; Leifeld et al., 2012), the build-up of decay end products (Fenner et al., 2005) and changes in the physical structure of the peat, such as the collapse of pore space (Boelter, 1969; Price et al., 2003). These changes limit the reactive surface of the peat and slows the diffusion of substrates (Clymo, 2016). All these factors may contribute to a slowing of peat decomposition. Early investigators noted the resistance of humified peat to further breakdown (e.g. Aiton, 1805) and this has been confirmed many times in the modern literature (Estop-Aragonés and Blodau, 2012; Jaatinen et al., 2007). Despite the decline in ER with time, it is important to note that ER is still elevated in comparison to a nearby undrained bog (Goodrich et al., 2017, Ratcliffe et al., 2019) and this is consistent with other sites internationally where ER remains greater in disturbed sites, compared with reference sites, for a decades or more despite highly humified peat (Waddington et al., 2002). Considerably more uncertainty surrounds the question of whether negative or positive feedbacks to decay will dominate the peatland carbon cycle after drying, when other processes are considered, i.e. will decay accelerate or slow with time? Despite the well-understood links between decay, litter quality and heterotrophic respiration, declining ecosystem respiration has seldom been directly observed in drying peatlands, with the possible exception being arctic peatlands as observed by Oechel et al. (2000).

Interestingly, ER has declined despite a number of confounding factors which may cause an increase in ER with time despite declines in the quality of peat (and plant matter). For example, nutrient enrichment (Bragazza et al., 2012; Minkkinen et al., 2007; Sulman et al., 2010). Changes in microbial ecology (Jaatinen et al., 2007; Mäkiranta et al., 2009) and increases in litter quality (Gogo et al., 2011; Laiho, 2006) can all be expected to promote decay. The effect of shrub expansion on heterotrophic respiration is still ambiguous (Walker et al., 2016; Ward et al., 2015). Ericoid shrubs may increase respiration through

microbial priming, modification of the microbial community (Artz et al., 2007), or decrease it through shading (Frost et al., 2018), burying of C through fast root turnover (Murphy and Moore, 2010) and possibly nutrient related competition with the microbial community (Ward et al., 2015), and accordingly it is unclear what the net effect may be.

In summary, GPP has increased across measurement periods, concurrent with the expansion of *E. pauciflora*. In contrast, negative feedbacks reducing ER appear to have become dominant after the 16-year interval between measurement periods. The exact mechanism for the decrease in ER is unknown, but physical and chemical changes to peat organic matter quality are a likely cause. Laboratory incubations of peat from Moanatuatua are consistent with this theory, as the rate of respiration was found to be considerably lower than other sites with less degraded peat (Hodge, 2002) and it is plausible that this would become more pronounced with time. However, the increase in the cover of the ericoid shrub *E. pauciflora* may also be a contributing factor to the decline in ER. The relatively steep response seen between temperature and ER anomalies (Figure 6) when considered in absolute terms, is consistent with that seen at similar temperatures in other studies (e.g. Makiranta et al., 2009) where temperature sensitivity can be similarly high at temperatures close to the annual average of 13.6 °C at Moanatuatua.

4.5.3 Change in NEP over time

There can be high interannual variability in NEP in undrained peatlands, as evidenced from long term datasets, for instance a standard deviation of 39 g C m-2 yr-1 (six years in Roulet et al., 2007) and 21 g C m-2 yr-1 (12 years in Peichl et al., 2014), therefore some natural degree of variation could be expected. However the standard deviation seen at Moanatuatua across the entire dataset, 139 g C m-2 yr-1, dwarfs that seen in long-term records, and fundamental differences, such as that seen in light response (Figure 5) and temperature response of ER (Figure 6) are evidence of fundamental changes occurring which are independent of the climatic conditions across the two periods.

The differences in NEP across the two time periods offer an insight into how peatlands respond to disturbance. The change in NEP at Moanatuatua, as the site adapts to lowered water tables, is consistent with data from other peatlands, where

losses of C due to disturbance or extreme weather events can be followed by a period of elevated C uptake, which may partially or wholly compensate for losses. This has been shown to be the case for drainage (Laiho, 2006; Minkkinen et al., 2002), fire (Wieder et al., 2009), and even sites that are undergoing restoration (Nugent et al., 2018; Strack and Zuback, 2013). Beyond the timescale measured, the sustained recovery of the CO_2 sink at Moanatuatua may depend on the water table returning to a normal range (e.g. 0-200 mm in Laitinen et al., 2008), limiting the duration of oxidative decay. The carbon fixed by NEP will remain highly vulnerable to climate and fire for as long as it remains as woody biomass in the canopy or in the oxygenated upper acrotelm (Frolking et al., 2014), which for a natural bog would usually be decades to centuries (Malmer and Wallén, 2004). At Moanatuatua, the water table consistently drops below 800 mm in the late summer (Figure 1) where the peat is approximately 1500 years old (Jara et al., 2017). It is unlikely that much, if any, of the carbon fixed today will persist if it is to undergo more than several centuries of oxidative decay. Rather than a sustained increase in carbon sequestration, the increase in NEP may actually represent a thickening of the aerobic acrotelm (Belyea and Clymo, 2001) and increasing woody biomass. Unless a shallowing of the water table occurs, the increasing NEP measured here will not necessarily translate to greater inputs of carbon into the catotelm.

We have shown the recovery of the contemporary carbon sink, after a 16-year interval, to have occurred despite lack of recovery to a shallow water table. It is possible the recovery of the carbon sink is a necessary first step towards a return of the ecosystem to its prior state. High NEP, if sustained, can be expected to remove nutrients from the ecosystem, by binding them within organic matter, which may eventually favour the more nutritionally conservative *E. robustum* over the shrub *E. pauciflora*. A corresponding return to the conservative evaporation regime typically seen with high *E. robustum dominance* (Campbell and Williamson, 1997) could lead to the eventual recovery of the water table, but this remains to be seen.

4.6 Conclusions

The CO2 sink in a drainage-affected restiad bog was found to have strengthened after an interval of 16 years, due to increasing CO_2 uptake via photosynthesis and reduced losses through ecosystem respiration. The changes observed could not be attributed to climatic variation, and temperature was found to be the only

significant contemporary driver of CO_2 flux anomalies, independent of time period, with warm temperature anomalies resulting in lower NEP. CO_2 uptake via GPP was greater in the recent time period, as was the response of NEE to light. We consider the expansion of the ericoid shrub *E. pauciflora*, which occurred in response to water table lowering, to be the most likely mechanism for this. We speculate that long term depletion of peat labile organic matter could be responsible for the decline in ER across time periods, however long-term changes in the decomposer community and mechanisms linked to the expansion of ericoid shrubs may provide alternate explanations.

The recovery of the peatland carbon sink at Moanatuatua demonstrated that internal processes have resulted in the strengthening, and recovery, of the CO_2 sink over the 16-year interval despite nutrient enrichment and a low and highly fluctuating water table. While these results appear to show a mechanism of long-term resilience of the ecosystem to water-table drawdown, the future viability of the bog will likely depend on the recovery of a shallower, more stable, water table regime of which there is not yet any sign. Understanding the timing and strength of internal feedbacks to external forcing remains a key challenge for peatland science and this understanding must be improved if we are to accurately predict how peatlands will respond to a changing climate.

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Chapter 5

Rapid carbon accumulation in a peatland following Late Holocene tephra deposition, New Zealand

5.1 Abstract

Contemporary measurements of carbon (C) accumulation rates in peatlands around the world often show the C sink to be stronger on average than at times in the past. Alteration of global nutrient cycles could be contributing to elevated carbon accumulation in the present day. Here we examine the effect of volcanic inputs of nutrients on peatland C accumulation in Moanatuatua bog, New Zealand, by examining a Late Holocene high-resolution C accumulation record during which powerful volcanic eruptions occurred, depositing two visible rhyolitic tephra layers (Taupo, 232 ± 10 CE; Kaharoa, 1314 ± 12 CE). Carbon accumulation rates since c. 50 CE, well before any human presence, increased from a background rate of 23 g C m^{-2} yr^{-1} up to 110 g C m^{-2} yr^{-1} following the deposition of the Taupo Tephra, and 84 g C m^{-2} yr^{-1} following the deposition of the Kaharoa Tephra. Smaller but nevertheless marked increases in C accumulation additionally occurred in association with the deposition of three andesitic-dacitic cryptotephras (each ≤ ~1 mm thick) of the Tufa Trig Formation. These five periods of elevated C uptake, especially those associated with the relatively thick Taupo and Kaharoa tephras, were accompanied by shifts in nutrient stoichiometry, indicating that there was greater availability of phosphorus (P) relative to nitrogen (N) and C during the period of high C uptake. Such P was almost certainly derived from volcanic sources, with P being present in the volcanic glass at Moanatuatua, and many of the eruptions described being associated with the local deposition of the P rich mineral apatite. We found peatland C accumulation to be tightly coupled to N and P accumulation, suggesting nutrient inputs exert a strong control on rates of peat accumulation. Nutrient stoichiometry indicated a strong ability to recover P within the ecosystem, with C:P ratios being higher than those at other peatlands in the literature. We conclude that nutrient inputs, deriving directly and indirectly from volcanic eruptions, appear to have been highly

important for C cycling in the past, and therefore that elevated nutrient inputs in the present day could offer a more plausible explanation than climatic variation for observed rapid C accumulation in peatlands in New Zealand and potentially elsewhere.

5.2 Introduction

The global peatland carbon (C) sink is vast, 644 GT by the most recent estimates (Yu, 2011; Dargie et al., 2017), and greater than all the C content of fossil fuels burnt since 1870 (~435 GT C, as cited in Le Quéré et al., 2018). Peatlands are thus very important for the global carbon cycle, and there is much interest in the controls of their C uptake and loss. Modern carbon sequestration in peatlands, measured over the past quarter-century or so, is often much higher than measurements of C accumulation rates (CAR) obtained from in peat cores representing longer time periods (Ratcliffe et al., 2018; Liu et al., 2019). In contrast to modern C flux measurements, long-term measurements of CAR, derived from peat cores, typically span several millennia or more and thus are heavily weighted towards the period before industrialisation began (~1750 CE). Since industrialisation, there have been major changes to atmospheric nitrogen (N) (Stevens et al., 2015) and phosphorus (P) deposition (Brahney et al., 2015; R. Wang et al., 2015), and nutrient-mediated effects have been cited as hypothetical explanations for the discrepancy between long-term and modern records of peatland C uptake (Turunen et al., 2004; Yu, 2012; Ratcliffe et al., 2018).

Volcanoes are known to deliver pulses of nutrients to ecosystems (Delmelle et al., 2015; Stewart et al., 2020), including peatlands (Wolejko and Ito, 1986; Hughes et al., 2013). In oceans, so-called volcanic fertilisation can cause large drawdown of atmospheric CO_2 (Delmelle et al., 2015). In lakes, the deposition of tephra (volcanic ash) may impact diatom assemblages and sedimentation rates (Harper et al., 1986; Abella, 1988; Einarsson et al., 1993; Urrutia et al., 2007; Hutchinson et al., 2019). However, the influence of volcanically-derived nutrients on peatland carbon cycling has seldom been explored. Volcanoes can deliver nutrients essential for plant growth, especially phosphorus, to ecosystems in three ways: (i) deposition of phosphatic compounds (presumably as PO_4^{3-}) formed from P-bearing aerosols derived from magmatic gases that are generated during eruptions; (ii) interaction of other acidic aerosols emitted during eruptions (including SO_2, HCl, NH_3, H_2S, and HF; e.g. Roberts et al., 2019) with P-containing volcanic

glass shards, pumice fragments, crystals (mineral grains), and lithics produced during the eruption; and (iii) by rapid dissolution of the particles of glass, pumice, and crystals, especially the phosphate-group mineral, apatite [$\underline{Ca}_{10}(\underline{PO_4})_6(OH,F,Cl)_2$], after their deposition by enhanced acid-induced hydrolysis that results in the release of constituent elements/ions (e.g. Cronin et al., 2003; Mahowald et al., 2008; Delmelle et al., 2015).

Ombrotrophic (rain-fed) peatlands, by definition, receive nutrients solely from atmospheric deposition and are among the most nutrient-poor ecosystems in the world (Damman, 1986). However, the effect of nutrient enrichment on ecology and carbon cycling is often unknown. Low concentrations of nutrient inputs can greatly increase primary productivity (Aerts et al., 1992; Lund et al., 2009) but, at high nutrient loading, peatland plants can also exhibit signs of toxicity (Sheppard et al., 2011) and ultimately undergo competitive displacement (Limpens et al., 2003). In turn, such displacement could lead to loss of ecosystem function and reduced C sequestration associated with more nutrient-demanding plant communities (Gogo et al., 2011). Additionally, nutrient enrichment may enhance C losses by accelerating the microbial breakdown of peat (Bragazza et al., 2012). Recently, it has become increasingly clear that there have been major changes to global nutrient cycling which are capable of affecting even geographically remote locations (Neff et al., 2008; Brahney et al., 2015). For ecosystems located close to agricultural nutrient sources, such changes may be even more pronounced (Tipping et al., 2014).

Volcanoes are potentially an important source of nutrients for peatlands close to active volcanic centres, but few studies have considered the role of volcanic nutrient sources in mire ecology and biogeochemical cycling. In Iceland, deposition of volcanic dust is a major control on wetland ecology affecting bird and insect populations through bottom-up differences in ecosystem productivity (Gunnarsson et al., 2015), while in Japan, Wolejko and Ito (1986) coined the term “tephrotrophic” to describe mires affected by tephra deposition. These tephrotrophic mires, although ombrogenous in that they received water only from rainfall, have maintained a fen-like plant community because of continued inputs of nutrients via tephra fall. Large areas of peatland in Te Ika-a-Māui, the North Island of Aotearoa/New Zealand, are located close to recently active volcanic centres, both rhyolitic and andesitic in composition (Fig 5.1; Wilson et al., 2009).

Peatlands analogous to those described by Wolejko and Ito (1986) also exist in New Zealand, where oligotrophic vegetation has been unable to achieve dominance in mires proximal to Mt Taranaki, an andesitic stratovolcano, due to continual fertilisation by frequent ash fall (McGlone et al., 1988; McGlone and Neall 1994). Delivery of nutrients, especially phosphorus (P), into New Zealand peatlands during the Late Holocene is likely because of the presence of P (reported as P_2O_5) in both volcanic glass shards (Gehrels, 2009) and the presence of the phosphate-rich mineral apatite that has been identified in distal tephra deposits of the past c. 2000 years in the Waikato region, including in lakes, such as Lake Rotomanuka near Moanatuatua bog, to the south of Hamilton (Fig 5.1; Lowe, 1988). Additionally, the 1995-1996 andesitic eruptions of Mt Ruapehu in central North Island (Fig 5.1) deposited fluorapatite, and analyses of tephra-samples (comprising mainly glass shards at distal sites) showed that P was present as a minor element (Cronin et al., 2003) (i.e., in quantities ≥ 0.1 wt%, following the quantitation terminology of Lowe et al., 2017). Similarly, distal tephra deposited in the Waikato region from the 1948 and 1975 andesitic eruptions of Mt Ngauruhoe contained P_2O_5 in minor or trace amounts (Allen, 1948; Nelson, 1975; Gehrels, 2009).

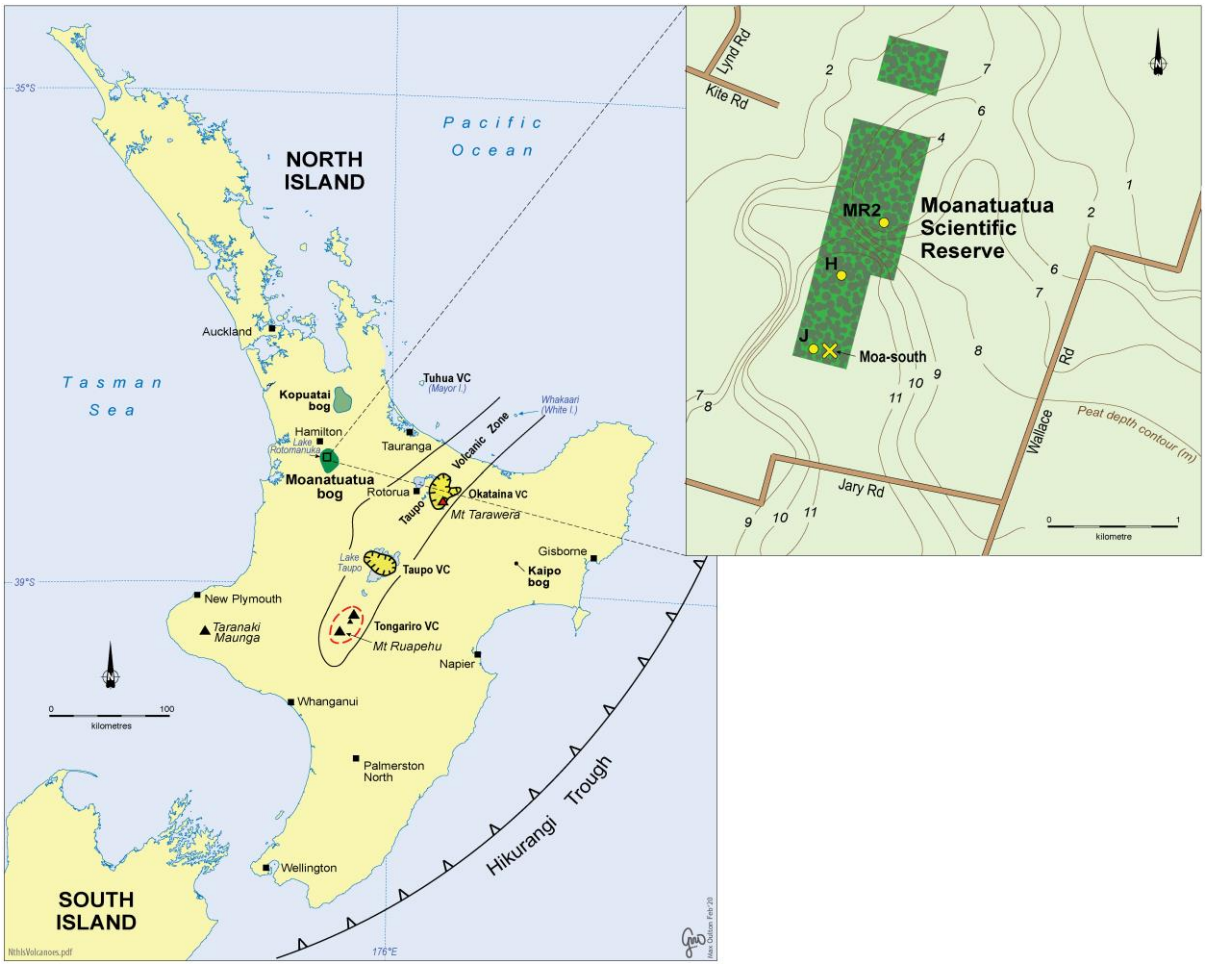

Figure 5.7. Map of volcanoes that have been active in North Island in the past c. 2000 years, including the sources of tephras recorded as either visible layers or cryptotephra deposits in Moanatuatua bog near Hamilton in the central Waikato region. The Hikurangi Trough marks subduction of the Pacific Plate beneath the Australian Plate on which North Island is situated. The inset map (right) shows our coring site, Moa-south, on the Moanatuatua Scientific Reserve, and that of Gehrels (2009), namely MR2. Coring sites of Haenfling et al. (2017) (H) and Jara et al. (2017) (J) are also noted. Most of the land beyond the reserve is agricultural farmland, with a blueberry orchard flanking Jary Road. Peat depths (in m) are from Davoren (1978).

Here we look at the effect of volcanic inputs on peatland carbon accumulation by studying the Late Holocene part – the past c. 2000 years – of a large ombrogenous bog, Moanatuatua, in northern New Zealand in a temperate, humid climate and which has received accessions of tephra-fall deposits. This peatland, and another close by (Kopuatai: Fig 5.1), have been found to have high CO_2 uptake in the present day, and this uptake remains strong despite inter-annual climatic variation (Goodrich et al., 2017; Ratcliffe et al., 2019a) and nutrient-related effects, associated with present-day land use, could offer an explanation for this CO_2 elevated rate in both bogs. Both sites are strongly phosphorus limited as indicated from N:P ratios in plant foliage (Clarkson et al., 2005) although P limitation is weakening at Moanatuatua over time (Clarkson in preparation). In this paper, we

examine peatland elemental accumulation rates, including C and elements relevant to growth, at a high chronological resolution to observe the effects on peatland elemental cycling.

We find that nutrient inputs, derived directly and indirectly from volcanic eruptions, have affected C cycling in the past, and therefore increased nutrient inputs could be primarily responsible for observed rapid C accumulation in peatlands where climatic limitations to growth are weak.

5.3 Methods and site description

5.3.1 Site description:

The Scientific Reserve on Moanatuatua bog is the remnant of a formally more extensive ombrotrophic peat bog (Fig 5.1). The reserve's (natural) vegetation is dominated by *Empodisma robustum* (Restionaceae), growing in association with *Epacris pauciflora* (Ericaceae) and *Sporadanthus ferrugineus* (Restionaceae) (de Lange et al., 1999; Ratcliffe et al., 2019b). In 1962 and again in 1972 two large fires broke out on the bog as the surrounding land was cleared for farming (Clarkson, 1997), and these fires were likely preceded by earlier burns also associated with land conversion (Reynolds, 1917; Cranwell, 1939). By 1979 the remaining Moanatuatua peatland was at its current size of ~140 ha (Matheson, 1979). The modern-day bog has undergone water table lowering and nutrient enrichment (Ratcliffe et al., 2019b) but, despite this, the peat-forming community in the reserve persists and the site remains a strong sink for carbon (Ratcliffe et al., 2019a).

5.3.2 Coring and core stratigraphy

The coring site (37.935970 S 175.366051 E), Moanatuatua south (Moa-south hereafter), was located 1.4 km south of a present-day CO_2 flux tower (Ratcliffe et al., 2019a) and close to coring sites for a number of previous palaeoecological and palaeoclimatological studies (Haenfling et al., 2017; Jara et al., 2017; Newnham et al., 2019). A Russian corer, 10 cm in diameter, was used (Belokopytov and Beresnevich 1955 in Jowsey, 1966), and cores were transferred to PVC tubing in the field, and wrapped in cling film and stored horizontally and refrigerated prior to subsampling. To supplement the findings we derived from our analyses of the Moa-south core, we also refer to cryptotephrostratigraphic work undertaken by

Gehrels (2009), reported in Gehrels et al. (2010), on a core (MR2) taken from a location less than 1.5 km from ours (Fig 5.1).

The stratigraphies of the Moa-south and MR2 cores, correlated using tephrochronology, are shown in Fig 5.2. Two visible rhyolitic tephras were identified: (1) Taupo Tephra, 2 cm thick, erupted in 232 ± 10 common era (CE) from Taupo Volcanic Centre (Hogg et al., 2012, 2019); and (2) Kaharoa Tephra, 5 cm thick, erupted in 1314 ± 12 CE from Mt Tarawera (in the Okataina Volcanic Centre) (Hogg et al., 2003). Three cryptotephras (which are defined as glass shard and/or crystal concentrations too sparse to be visible to the naked eye as layers: Lowe, 2011) were identified in the peat in core MR2 by Gehrels (2009, 2010) as andesitic-dacitic members Tf4 (erupted c. 750 CE), Tf5 (erupted c. 1200 CE), and Tf6 (erupted c. 1250 CE) of the Mt Ruapehu-derived Tufa Trig Formation (Donoghue et al., 1997). They were identified (in MR2) by peaks in counts of brown glass shards, the shards being characterised for major element compositions using methods reported in Gehrels et al. (2006). The approximate dates associated with the cryptotephras in MR2 are based on age data in Donoghue et al. (1997), Gehrels (2009), and Zawalna-Geer et al. (2016). It should be noted that there is some uncertainty as to the exact deposition horizons of TF5 and TF6, where the peaks in shards were not pronounced, and there was a wide distribution of tephra over a ~10 cm interval Gehrels (2009, 2010).

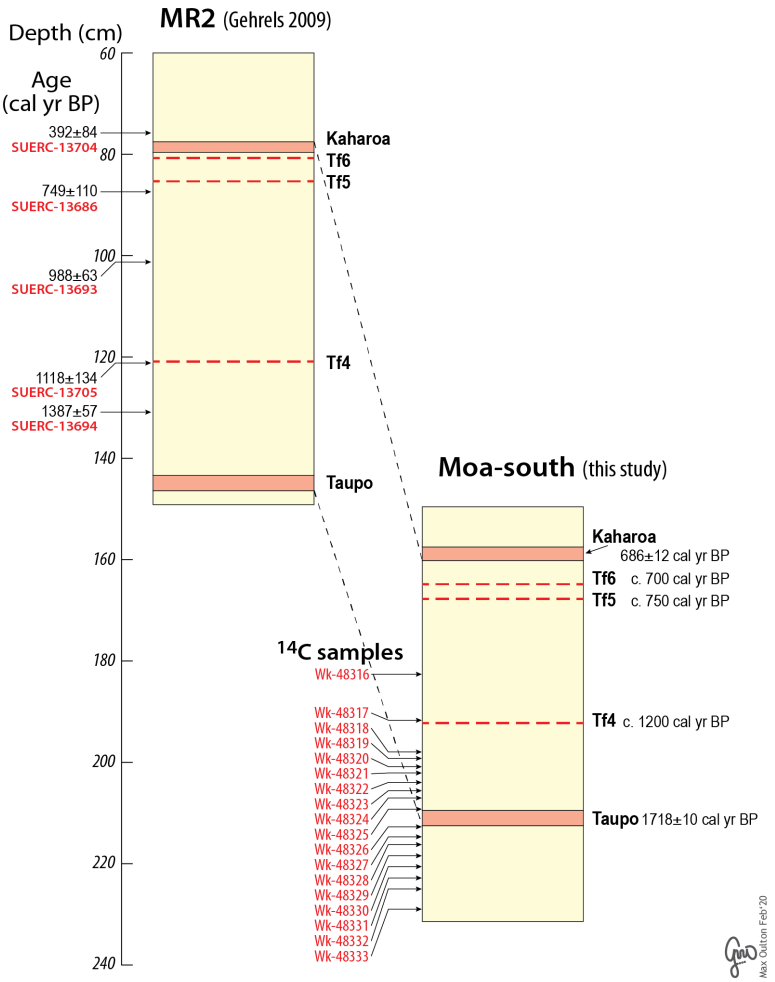

Figure 5.2. Stratigraphy of Moanatuatua south core (Moa-south) and the corresponding section of core MR2 of Gehrels (2009). The two visible tephras linking the records are shown as orange bands; the three cryptotephras are depicted as red dashes. Calibrated radiocarbon ages (95% probability ranges) obtained for core MR2 are given (from Gehrels, 2009). Note there is some offset in depth between the two cores, see Shearer (1997) for more information on how tephra depth varies in Moanatuatua bog. Sampling positions for radiocarbon ages obtained on the Moa-south core (this study) are also shown (see Table 5.1). SUERC = prefix for radiocarbon ages obtained at the NERC lab, Scotland; Wk = prefix for radiocarbon ages obtained at the Waikato lab, Hamilton, New Zealand.

5.3.3 Bulk density

Bulk density was measured at 1-cm vertical resolution, with volume calculated using the water displacement technique (Chambers et al., 2011) and then the dry weight was measured after drying the samples at 55 °C until at a constant weight was attained.

5.3.4 C/N

Samples were oven-dried at 55 °C and homogenised using a steel-ball mill which was cleaned and dried between samples to avoid contamination. Dried peat with a mass of 0.02 g was weighed out and analysed for C and N content using a Vario

El cube CHNOS Elemental Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) with acetanilide standards.

5.3.5 Elemental analysis by inductively coupled plasma-mass spectrometry (ICP-MS)

The core was subsampled for ICPMS analysis at 1-cm intervals. Care was taken to avoid contamination and sample preparation was carried out in a random order to limit the possibility of false trends appearing as a result of contamination. Dried samples were coarsely homogenised by hand and 0.5 g of dried sample was ashed at 450 °C for 4 hours following Yafa and Farmer (2006). One millilitre of concentrated nitric acid was added to the ash and samples were digested on a heat block at 80 °C for 2 hours. Samples were made up to 50 ml with de-ionized water and centrifuged at 1800 rpm for 10 minutes. Ten millilitres of the sample was then decanted and used for ICPMS analysis for 27 inorganic elements: B, Na, Mg, P, S, K, Ca, Si, V, Cr, Mn, Co, Ni, Cu, Zn, Sr, As, Se, Ag, Cd, Ba, Pb, Al and U. Also analysed were Hg, Fe, and Ni but the results for these are considered less reliable due to volatilisation (Hg) and potential contamination from the sampling and laboratory process (Fe and Ni). Analyses were undertaken using an Agilent 8900 ICP-MS (Agilent Technologies, Santa Clara, USA) controlled by MassHunter Workstation (version 4.5). Sample introduction occurred via an SPS4 autosampler (Agilent Technologies, Santa Clara, California, USA) and PVC tubing (Pulse Instrumentation, Mequon, Wisconsin, USA). A 0.05-0.1 mL/min micromist U-Series nebuliser (Glass Expansion, Melbourne, Australia) was attached to a quartz cyclonic spray chamber followed by a quartz torch with 2.0 mm injector (Agilent Technologies, Santa Clara, USA). Following the plasma, the sample was introduced to the rest of the instrument via a nickel sampler and skimmer cone, followed by an extraction omega lens (Agilent Technologies, Santa Clara, USA). The ICP-MS was optimized to maximum sensitivity ensuring oxides and doubly-charged ions were less than 2%.

A five-point calibration curve, consisting of concentrations between 0.1 and 500 ppb was prepared for all trace elements using stock standard IV71-A (Inorganic Ventures, Christiansburg, USA). A separate calibration curve, consisting of concentrations between 100 and 10,000 ppb, was prepared for major elements (Ca, Si, P, S, K, Fe) using single-element standards (Inorganic Ventures, Christiansburg, USA). An internal standard consisting of Sc, Ge, Rh, Te, and Ir

was utilized to correct for instrumental drift. Standards were analysed every 20 samples and re-calibration was performed every 100 samples. Blank samples were analysed every 10 samples to ensure minimal carryover between samples.

5.3.6 Chronology and age-depth model

5.3.6.1 Radiocarbon samples

Subsamples of wet peat (Fig 5.2) were disaggregated using the hot NaOH method (Mauquoy et al., 2010) and sieved at 120 μm, discarding the filtrate. Above-ground material, mainly plant stems and charcoal, was manually separated under a microscope and was cleaned using de-ionized water. Combinations of macroscopic charcoal, *Empodisma* stems, and wood was used for radiocarbon (^{14}C) dating (Table 5.1, Fig 5.2). Material for dating was stored in de-ionized water, mildly acidified with H_2SO_4 to preserve the samples, and then submitted to the Waikato Radiocarbon Dating Laboratory for accelerator mass spectrometry (AMS) dating, using the Keck Carbon Cycle Accelerator Mass Spectrometer facility at the University of California, Irvine, USA.

5.3.6.2 Age-depth model

Calibrated ^{14}C ages were combined with the high-precision dates for the two visible tephra layers, Kaharoa Tephra at 158 cm depth (1314 ± 12 CE), and Taupo Tephra at 210 cm depth (232 ± 10 CE) (Fig 5.2). The tephras were identified in the field by their distinctive physical properties and their stratigraphic superpositions in the core near the bog surface. Both have been characterised or 'fingerprinted' previously in studies on numerous lakes and bogs in the Waikato region using their ferromagnesian mineralogical assemblages and glass-shard major element compositions, including in Moanatuatua bog itself as reported by Gehrels (2009) and Newnham et al. (2019) (see also Green and Lowe, 1985; Lowe, 1988; de Lange and Lowe, 1990; Hodder et al., 1991; Gehrels et al., 2006). The newly acquired ^{14}C dates support the identifications. The lowest C content of the peat was used to indicate the specific point (instant in time) at which the tephras were deposited, with 16.9% C at 158 cm and 19.9% C at 210 cm, compared to the core average of 47.1% (Table 5.2). The age-depth model was constructed using the Bayesian software BACON 3.3.3 (Blaauw and Christen, 2011) modelled against SHCal13 of Hogg et al. (2013). The prior accumulation rate was set at 10 yr cm^{-1} and a 1-cm section depth was specified, and the default

sample size was increased to 14000 to obtain a satisfactory mix of 1000 Markov Chain Monte Carlo iterations. Other accumulation and memory priors were set to the default values following Goring et al. (2012).

5.3.6.3 C accumulation rates

C accumulation rates were calculated using the measured carbon content of each 1-cm slice divided by the modelled age difference between the top and bottom of the slice that was produced using the age-depth model.

5.4 Results

5.4.1 Chronology and age-depth model

All dates were included in the initial age-depth model but the optimal model did not pass through dates Wk-48328 and Wk-48329, which were identified as outliers, and so were not included in the final model. BACON is designed to infer periods when a hiatus in the sequence is likely to have occurred, with short hiatuses being progressively more likely. However, despite a period of slow peat accumulation at 187–191 cm depth, no hiatus was detected, i.e. the slow accumulation rate was plausible. The model displayed considerable variation in the peat accumulation rate (Table 5.2), most notably with periods of rapid accumulation at depths of 207–220 cm and 150–161 cm.

Table 5.1. Radiocarbon ages used to construct the chronology for the Moanatuatua south core (see also Fig 5.2).

Laboratory no. (Waikato)	Depth (cm)	Macrofossils selected for AMS dating	Conventional radiocarbon age (^{14}C yrs BP ± 1σ)	'Best estimate' weighted mean age/date (CE)‡	2σ calibrated date range (CE)
Wk48316	182	*Empodisma* stem	1035 ± 15	1039	916-1122
Wk48317	191	Macro charcoal*	1562 ± 19	592	490-591
Wk48318	197	Macro charcoal	1677 ± 19	431	383-489
Wk48319	198.5	Macro charcoal	1668 ± 19	399	365-440
Wk48320	201	Macro charcoal	1737 ± 19	366	336-399
Wk48321	202	Macro charcoal	1832 ± 19	349	325-377
Wk48322	204	Macro charcoal	1792 ± 19	315	283-347
Wk48323	206	Macro charcoal	1790 ± 19	292	252-292
Wk48324	208	Macro charcoal	1815 ± 20	280	244-310

Wk48325	209.5	Macro charcoal	1782 ± 20	267	231-301
Wk48326	211.5	*Empodisma* stem	1678 ± 14	259	229-294
Wk48327	214	Wood with external bark	1864 ± 16	251	218-283
Wk48328[δ]	215.5	*Empodisma* stem	1480 ± 15	244	204-274
Wk48329[δ]	218	*Empodisma* stem	1689 ± 14	238	183-264
Wk48330	220	*Empodisma* stem	1838 ± 15	232	162-257
Wk48331	222	*Empodisma* stem	1654 ± 14	211	151-236
Wk48332	224	*Empodisma* stem	1888 ± 14	190	134-228
Wk48333	228.5	*Empodisma* stem	1962 ± 15	110	60-188

*Macro = >120 μm.

[‡]The weighted mean age (or date in this case) is a single-age representation that takes into account the general outcome of all MCMC iterations in the Bacon modelling (Blaauw and Christen, 2011).

[δ]These dates were identified as outliers and rejected from the BACON modelling (Fig 5.3).

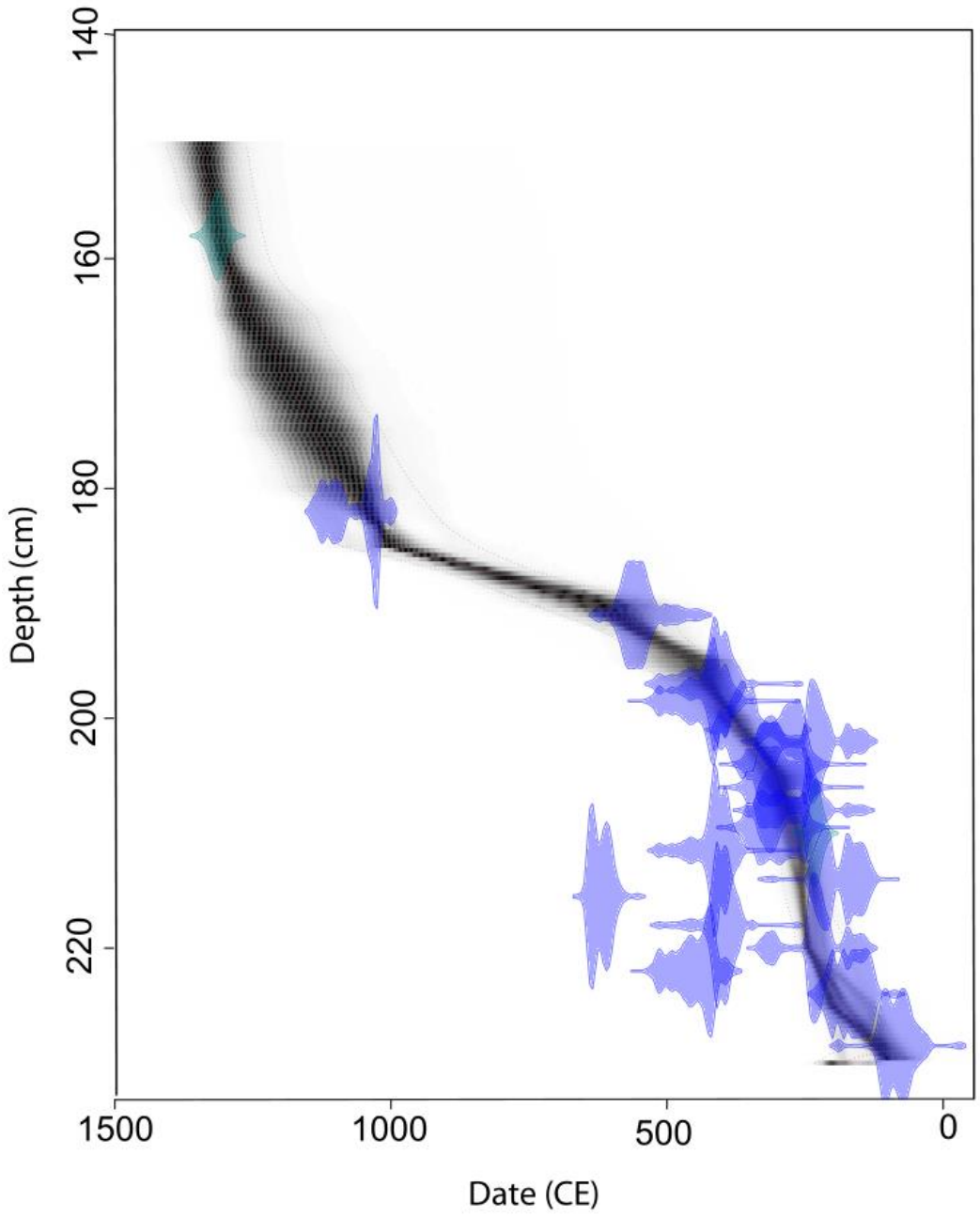

Figure 5.3. Age-depth model (in calendar years plotted as dates) for the core produced using Bayesian modelling via BACON (Blaauw and Christen, 2011), and 14C ages as listed in Table 5.1. Dates adopted for the two visible tephras (green shapes) are Taupo, 232 ± 10 CE (Hogg et al., 2012, 2019), and Kaharoa, 1314 ± 12 CE (Hogg et al., 2003). Blue shapes represent the statistical probability of age/depth associated with each date, and the back/grey shading represents the 95% confidence interval of the preferred age/depth model.

5.4.2 Carbon accumulation and changes in physical and chemical properties in the Moa south core.

The CAR of the Moa-south core (figure 4) was found to vary considerably across the 1200-year-long time period considered.

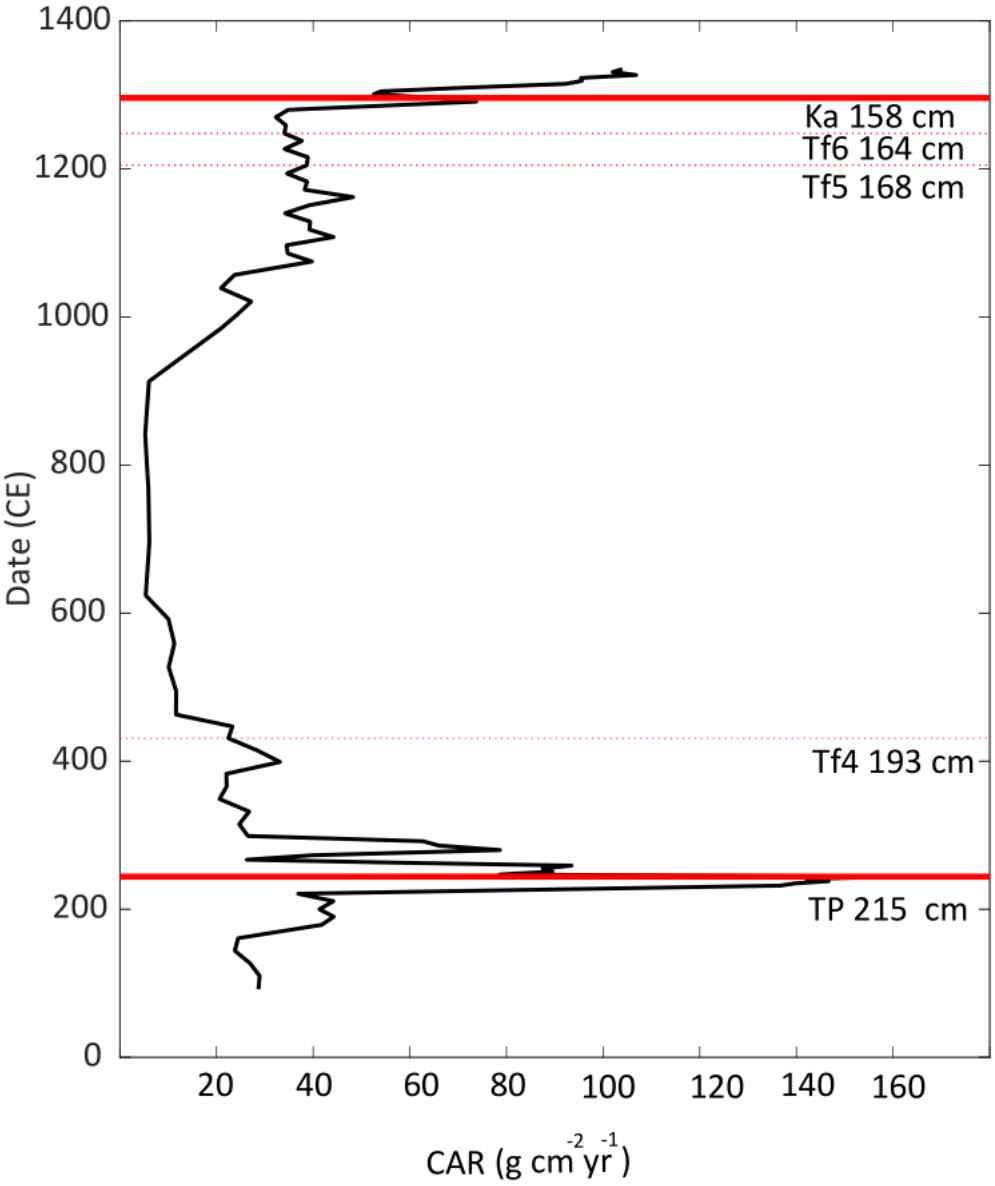

Figure 5.4 Carbon accumulation rate (CAR) in Moa South core plotted against calendar date. The isochrons provided by the Taupo (TP) and Kaharoa (KA) tephras are represented by the two red solid horizontal lines, and the inferred positions of the Tufa Trig cryptotephras (Tf4–6) are marked by dotted lines the names and depth of these tephras have been added as annotations.

We defined six zones within which the CAR was relatively consistent (Table 5.2) and describe these in the following section.

Zone 1:

Zone one began around 90 CE at 230 cm depth, approximately 140 years before the Taupo Tephra was deposited. This zone contained 9 cm of peat, CAR was high, and C content was lower (Table 5.2) than that in other zones where volcanic inputs were not so clearly evident. Bulk density in this zone was close to the core average (Table 5.2).

Zone 2:

This zone began at 221 cm, about 6 cm below the point where the influence of the Taupo Tephra became clearly evident in the sequence (215 cm depth), CAR increased sharply to 140-160 g C and dropped slightly to between 80 and 100 cm before briefly dipping to 25 g C m^{-2} yr^{-1} at the peak of the tephra-derived glass-shard abundance (210 cm). Elevated CAR was evident to 205 cm, equivalent to ~300 CE, where the zone ends (Table 5.2). Bulk density was variable in this zone but peaked at 208 cm just after the point of maximum glass-shard deposition where it reached 0.13 g cm^{-3} (data not shown).

Zone 3

Zone 3 begins at 204 cm and ends at 196 cm with CAR consistently between 20-27 g C m^{-2} yr^{-1}, except a peak between 200 and 197 where CAR increased to 33 g C m^{-2} yr^{-1} at 199 cm, essentially matching the inferred location (in corresponding core MR2 of Gehrels, 2009) of cryptotephra Tf4 at 197 cm (Fig 5.4), and the large spikes in uranium, copper, and lead concentrations also at 197 cm depth (Figure 5.5). Zone 3 ends at ~450 CE.

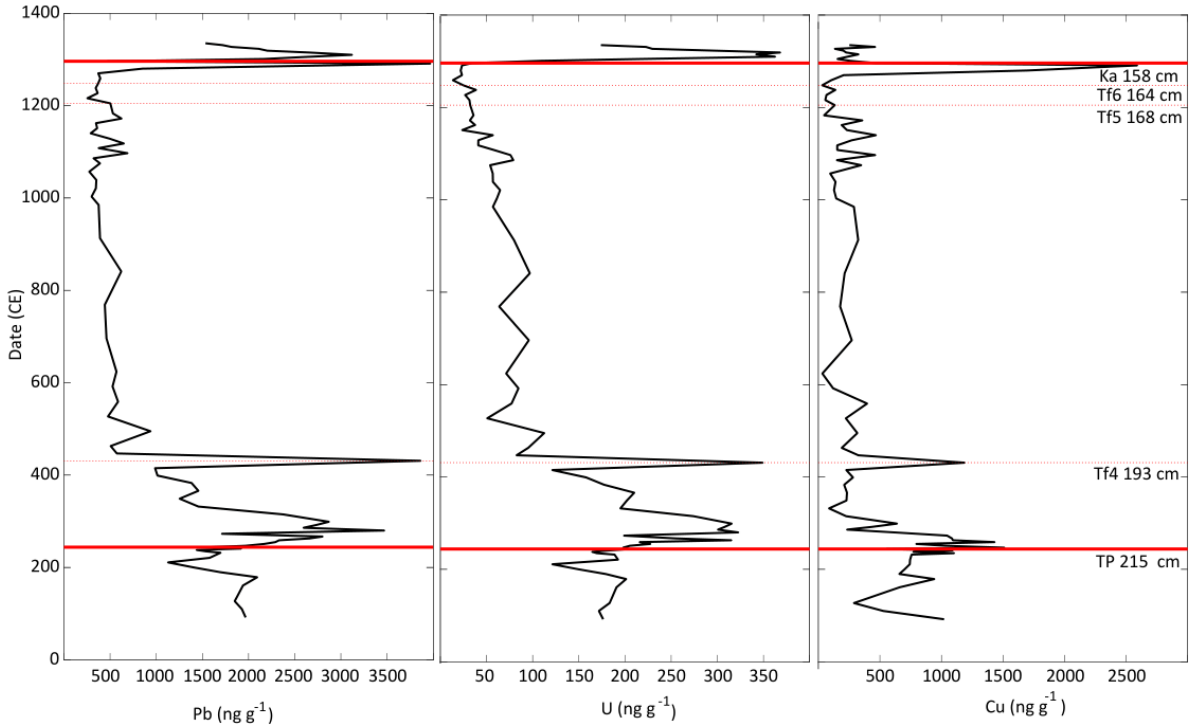

Figure 5.5 Lead (Pb), uranium (U) and copper (Cu) concentrations plotted against age (date in calendar years). Tephra or cryptotephra deposits are shown as solid or dashed horizontal lines, respectively, as described in Fig 5.4 and the names and depth of these tephras have been added as annotations.

Zone 4:

Zone 4 begins at 195 cm and ends at 186 cm, representing a period of about ~450 years in duration. During this period, CAR was at its lowest, varying between 13 g C m^{-2} yr^{-1} and 5 g C m^{-2} yr^{-1} (Figure 4), bulk density was also at its lowest, but C content was greatest – between 53 % and 56% – the peak occurring at 189 cm (Table 5.2).

Zone 5:

Zone 5 begins at 185 cm and continues to 161 cm, covering a period of about 300 years. The CAR was found to increase steadily, varying between 20 and 49 g C m^{-2} yr^{-1} (Figure 4). No clear trends in uranium, copper, and lead concentrations were seen in the early part of the zone (Figure 5), but there was a drop in the C:P ratio of about 800 at 182 cm (Figure 4), indicating greater P abundance in the early part of the zone. Towards the end of the zone, at 168 and 164 cm, the closely-spaced Tf5 and Tf6 cryptotephra deposits occur (as inferred from the correlative core MR2 of Gehrels, 2009). Their inferred positions are close to a small peak in uranium, copper, and lead at 165 cm, and also close to a much larger peat at 162 cm nearly 4 cm below the Kaharoa Tephra (Figure 5).

Zone 6:

Zone 6 is primarily affected by the deposition of the Kaharoa Tephra, CAR varies between 73 and 107 g C m^{-2} yr^{-1}, and, as with the Taupo Tephra in Zone 2, and there is a small dip in CAR, to 52 g C m^{-2} yr^{-1}, which corresponds with peak tephra deposition (Figure 4). This zone is also characterised by the highest concentrations of uranium, copper, and lead seen in the record (Figure 5) and the lowest C:P and N:P ratios (Figure 6).

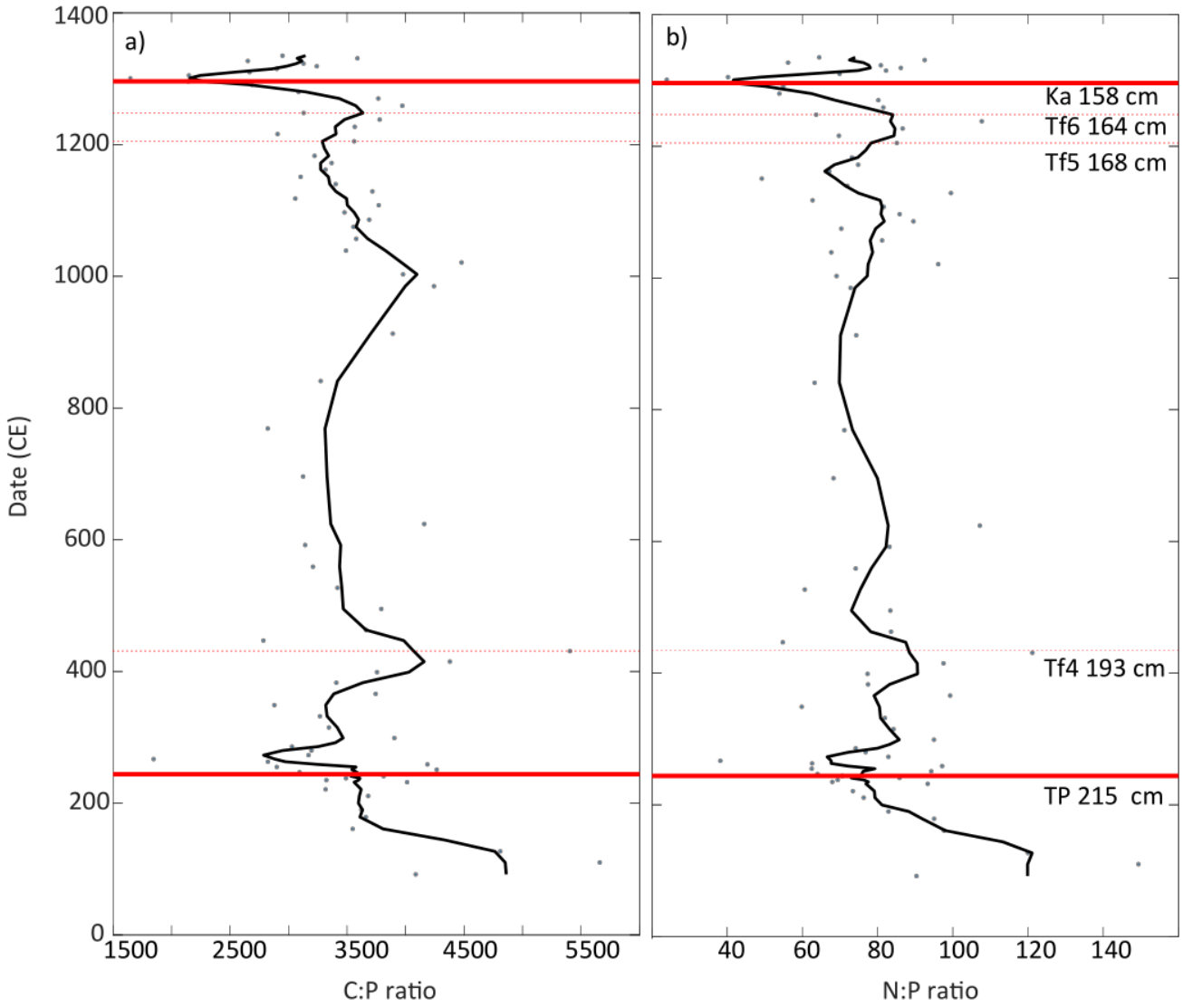

Figure 5.6. (a) C:P ratio plotted as points, with a ten-sample moving mean plotted as a line; (b) N:P ratio plotted as points, against age (date in calendar years), with a ten-sample moving mean plotted as a line. Tephra or cryptotephra deposits are shown as solid or dashed horizontal lines, respectively, as described in Fig 5.4 and the names and depth of these tephras have been added as annotations.

Table 5.2. Summary of peat, carbon, and phosphorus accumulation rates along with C:N ratios and measurements of bulk density and C and N contents.

Zone	Depth range (cm)	Date range (95% prob) CE	Bulk density g cm^{-3}	Carbon accumulation rate g C cm yr^{-1}	Phosphorus accumulation rate g P cm yr^{-1}	C %	C:P	P:N
Z6	160-150	1291-1335	0.109±0.015	83 ±20	0.031±0.004	34 ± 10	2704 ± 556	83 ± 22
Z5	185-161	985-1291	0.076±0.007	35 ±7	0.010±0.003	54 ± 6	3550 ± 383	97 ± 14
Z4	195-186	463-985	0.071±0.008	8 ± 3	0.003±0.00	54 ± 1	3436 ± 433	96 ± 14
Z3	204-196	315-436	0.090±0.018	24 ± 6	0.001±0.002	46 ±6	3663 ± 765	104 ± 19
Z2	221-205	221-315	0.093±0.019	86 ± 44	0.026±0.012	41 ±9	3374 ± 608	96 ± 16
Z1	230-222	92-222	0.089±0.005	34 ± 9	0.001±0.003	51 ±1	4153 ± 798	122 ± 25
All	230-150	92-1335	0.087±0.018	48 ± 36	0.015±0.012	47 ±9	3448 ± 659	98 ± 19

5.4.3 Carbon accumulation and elemental concentrations

ICPMS analyses of elements resulted in counts above the detection limit for almost all elements considered, except for silver and cadmium for which approximately half the analyses were below the detection limit and mercury which was lost during sample ashing. and thus was consistently below the detection limit The results of the analyses are presented in full in the Supplementary Data. In order to investigate how these elements varied with CAR, we performed linear regressions between all the elements we had measured and the CAR (Figure 7). The elements with the greatest correlation, uranium, lead, and copper, but excluding Al which is known to be mobile at low pH, were then plotted against CAR (Figure 5). Elements including aluminium, lead, uranium, copper, chromium, cobalt, and potassium correlated positively with CAR whereas silicon, barium, calcium, strontium, and magnesium correlated negatively and, in the cases of calcium, strontium and magnesium, their correlations were quite strong.

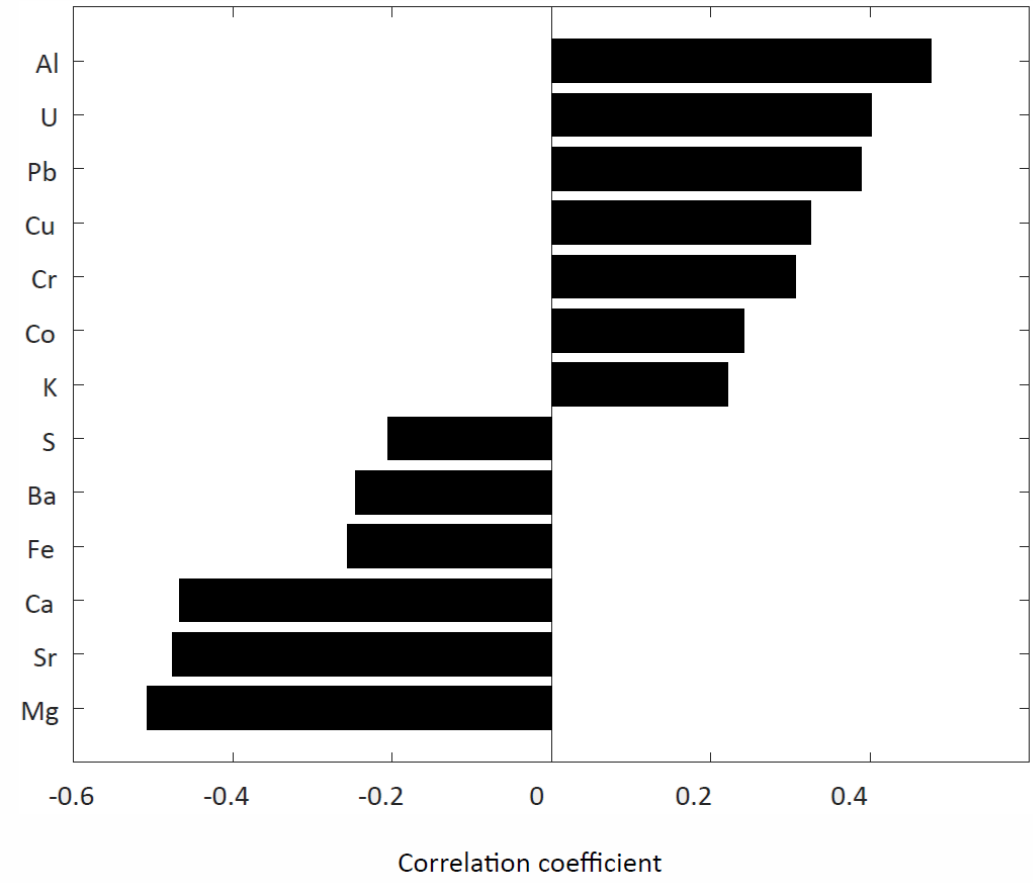

Figure 5.7. Correlation coefficients of C accumulation rates and elemental concentrations for linear regressions where P <0.05.

5.5 Carbon, nitrogen and phosphorus accumulation and stoichiometric ratios

Carbon, nitrogen, and phosphorus accumulation rates followed a similar pattern to each other and were highly correlated (Figures 8 and 9), maintaining consistent stoichiometric ranges throughout most of the time series (C:P of 3500 and P:N of 80), with the exception of the two visible-tephra depositional events (Taupo and Kaharoa), and the short period at the very start of the sequence between ~90 and ~220 CE. Carbon-to-phosphorus ratios were at their highest in the earliest part of the time series, around 4000, then declined greatly with the deposition of the Taupo Tephra to around 3300 before increasing and stabilising to 3500, and then declining again to around 2700 at the time of deposition of the Kaharoa Tephra (Figure 8).

Rates of C accumulation varied from 160 g C m^{-2} yr^{-1} at ~244 CE (216 cm depth) to 5.2 g C m^{-2} yr^{-1} at ~840 CE (187 cm depth). Extremes in CAR were mirrored by those of P, 0.04 g C m^{-2} yr^{-1} at ˜244 CE (216 cm depth) and 0.001 g C m^{-2} yr^{-1} at 627 CE (190 cm depth) (Figure 8), and also N accumulation rate of 4.0 g C m^{-2} yr^{-}

^{1} at ~244 CE (216 cm depth) and 0.1 g C m^{-2} yr^{-1} at ~840 CE (187 cm depth) (Figure 8).

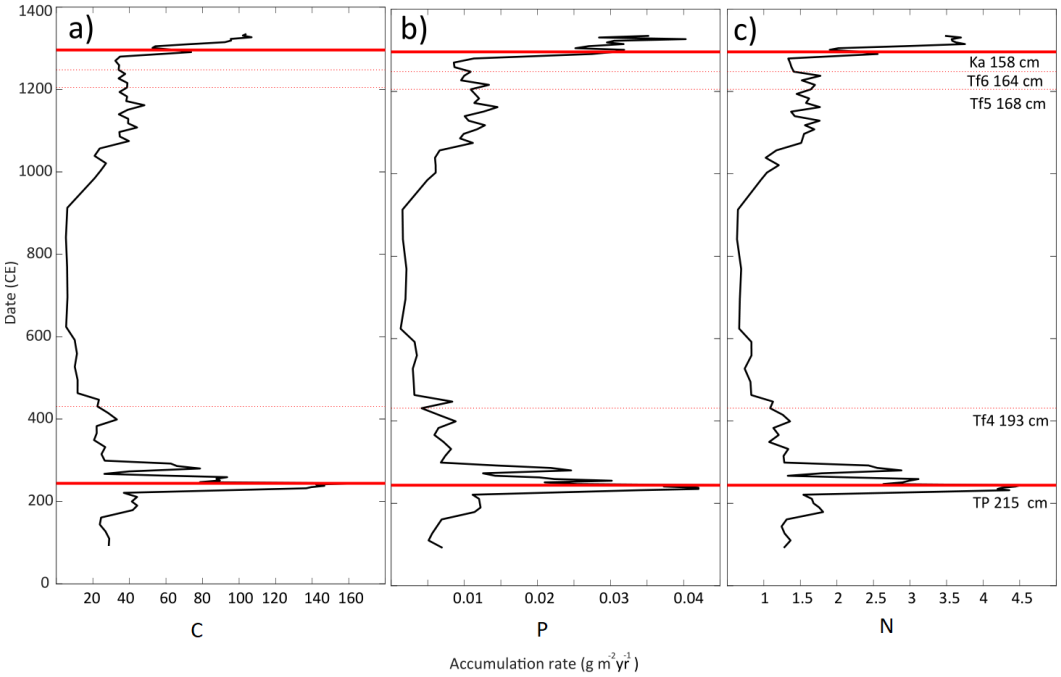

Figure 5.8. Accumulation rates of elemental Carbon (a), phosphorus (b), and nitrogen (c), each plotted against age (date in calendar years) and depth. Tephra or cryptotephra deposits are shown as solid or dashed horizontal lines, respectively, as described in Fig 5.4. The names and depth of these tephras have been added as annotations.

5.6 Correlations between C, N, and P accumulation rates

Carbon accumulation rates were found to have a strong positive linear correlation with N (R^2 0.98) and P (R^2 0.91) accumulation rates (Figure 9), and this was most pronounced in the lower, 'typical' range of CAR 0-60 g C m^{-2} yr^{-1}, with greater residuals at high CAR > 60 g C m^{-2} yr^{-1}.

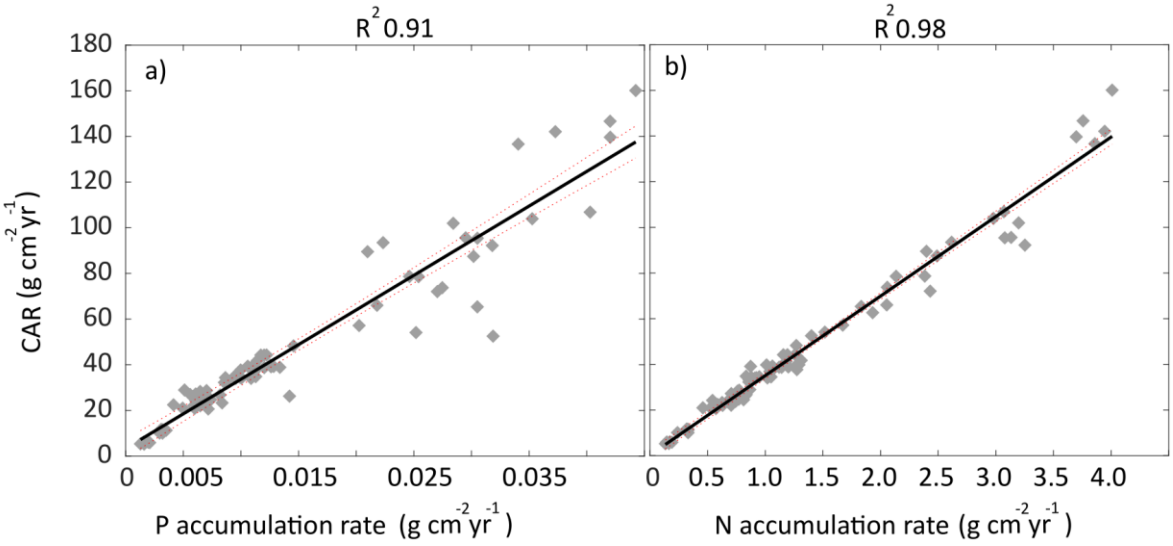

Figure 5.9 (a) Linear regression of elemental P accumulation rate and C accumulation rate (CAR); (b) Linear regression of elemental N accumulation rate and C accumulation rate.

5.7 Discussion

The deposition of the two visible rhyolitic tephra layers, Taupo (Tp) (232 ± 10 CE) and Kaharoa (Ka) (1314 ± 12 CE) caused CAR to increase from a background of 23.1 g C m^{-2} yr^{-1} (Table 5.2) to a maximum sustained rate of 110 g C m^{-2} yr^{-1} after Tp and 84 g C m^{-2} yr^{-1} after Ka. Carbon accumulation rates following the deposition of Tp and Ka were much higher than are typically seen in peat cores (e.g. 22 g C m^{-2} yr^{-1} was recorded for southern peatlands by Yu, 2011), and are more typical of rates for contemporary peatland CO_2 uptake – for example, a rate of 74 g C m^{-2} yr^{-1} was calculated from 24 site-years across six peatlands by Lu et al. (2017).

Additionally, a small increase in CAR, to 30-35 g C m^{-2} yr^{-1}, was evident at c. 420 CE, with concurrent spikes in uranium, lead, and copper (Figure 5). This increase may relate to the deposition of the dacitic Tufa Trig tephra, Tf4, derived from Mt Ruapehu (Donoghue et al., 1997), identified as a cryptotephra in core MR2 in Moanatuatua bog by Gehrels (2009) (Fig 5.2; Table 5.3). Possible increases in CAR were also evident in Zone 5 in which the closely-spaced andesitic-dacitic Tufa Trig tephras Tf5 and Tf6 (aged c. 1200 and c. 1250 CE, respectively) were identified in nearby core MR2 (Fig 5.2; Table 5.3).

Table 5.3. Oxide contents of volcanic glass shards, expressed as mean weight percent (± 1 sd), derived by electron microprobe analysis of tephras and cryptotephras in core MR2*.

Tephra	SiO_2	Al_2O	TiO_2	FeO†	MnO	MgO	CaO	Na_2O	K_2O	P_2O_5	H_2O^{δ}	*n*
Kaharoa	77.78	12.13	0.09	0.8	0.05	0.08	0.44	4.18	4.11	0.00	1.11	71
	(2.27)	(1.17)	(0.14)	(0.73)	(0.05)	(0.25)	(0.74)	(0.42)	(0.43)	(0.04)	(0.96)	
Tf6	63.09	14.46	1.12	6.52	0.12	2.07	4.93	3.78	2.79	0.25	1.37	22
	(0.39)	(0.28)	(0.11)	(0.25)	(0.11)	(0.22)	(0.26)	(0.22)	(0.20)	(0.08)	(0.29)	
Tf5	68.34	13.53	1.03	5.29	0.11	1.18	3.60	3.7	3.03	0.23	1.21	17
	(1.77)	(1.15)	(0.16)	(0.94)	(0.06)	(0.31)	(1.03)	(0.24)	(0.81)	(0.05)	(0.37)	
Tf4	66.38	14.61	0.92	4.58	0.07	1.06	3.70	4.05	3.32	0.20	2.04	6
	(2.14)	(1.99)	(0.12)	(0.99)	(0.08)	(0.44)	(1.74)	(0.30)	(1.42)	(0.03)	(0.49)	
Taupo$^{\Sigma}$	75.69	12.77	0.25	1.90	0.10	0.25	1.52	4.26	2.93	0.03	3.08	61

	(0.82)	(0.29)	(0.06)	(0.30)	(0.07)	(0.06)	(0.19)	(0.31)	(0.37)	(0.02)	(1.52)

* Data (normalised to 100% loss-free basis) are from Gehrels (2009). Analyses were acquired at the NERC Tephra Analytical Unit, University of Edinburgh, in February and June 2007. Mean values for independently characterized laboratory standards, TB1G and Lipari, are available in Newnham et al. (2018).

† Total Fe expressed as FeO

$^{\delta}$ 'Water' by the difference between the original analytical total and 100

$^{\Sigma}$Further electron microprobe analyses on glass from Taupo Tephra in Moanatuatua bog are reported by Newnham et al. (2019, p. 384).

n, number of individual shards analysed in generating the mean.

Carbon accumulation rate has rarely been measured in peatlands across time periods spanning tephra deposition events, with the only other example of which we are aware being reported for a bog in Hokkaido, Japan (Hughes et al., 2013), where CAR above 100 g C m^{-2} yr^{-1} occurred after deposition of a rhyolitic tephra (B-Tm) erupted from Changbaishan (or Baitoushan) volcano located more than 1000 km away on the China/North Korea border. In that case, elevated CAR, linked to P inputs, was found to be sustained for about 300 years rather than the ~80 years we found here, but this apparent extended period could be, in part, due to coarser dating resolution used by Hughes et al. (2013). The rapid CAR we found here, and that in Hughes et al. (2013), would be unlikely to be detected in typical paleoecological studies with around one date per 1000 years (Payne et al., 2016). Therefore, we do not consider the paucity of examples in the literature to preclude this phenomenon from being more widespread.

Modern experiments and palaeoecological reconstructions suggest that the impacts of tephra on peatland plant mortality can be inconsistent (Payne and Blackford, 2008, 2005). Vascular plants can remain unaffected by tephra falls up to 6 cm thick (Hotes et al., 2006). Much thicker deposits than reported here for Moanatuatua – for example, a 22-cm thick tephra layer in the montane Kaipo bog in New Zealand (Fig 5.1) – may cause disruption of the plant community (Giles, 1999). Beyond the immediate disturbance effect, the nutrient impact may be of greater importance for CAR. Phosphorus is one of the key limiting nutrients in ombrotrophic peatlands (Aerts et al., 1992; Clarkson et al., 2005), with inputs

coming solely from atmospheric inputs, both direct and indirect via rapid weathering of atmospheric dust.

The fallout from two Late Holocene volcanic eruptions in North Island, including the Taupo event, have been previously associated with increased lake primary productivity at a distal site (Lake Poukawa) in Hawke's Bay (Fig 5.1), and the authors concluded this enhancement was likely to be driven by P (Harper et al.,1986). Our data, involving five tephra or cryptotephra deposits, also indicate that increased P input is likely to be the mechanism behind the increase in C accumulation. This mechanistic explanation is evident from the stoichiometric ratios, which shifted towards greater P relative to C and greater P relative to N at the time of deposition of Tp and Ka tephras, and also at close to the inferred times of deposition of cryptotephras Tf4, Tf5, and Tf6 (Figure 9). Although we did not find evidence of a change in absolute (numerical) P concentration, such a change is not unexpected given that P is rapidly utilised and re-cycled by peatland plants within the shallow surface layers of bogs, moving up vertically through the peat (M. Wang et al., 2015). Because of rapid re-cycling within the peatland ecosystem, P accumulation rate is considered a more reliable indicator of P inputs than P concentration (M. Wang et al., 2015). In contrast, elements that are relatively immobile and not biologically utilised, such as lead, uranium, and copper (Novak et al., 2011; Mikutta et al., 2016), increased in absolute (numerical) terms at times of high CAR (Figure 5) and, moreover, were positively correlated with CAR, increasing at the time of the eruptive events.

As noted earlier, volcanic eruptions add nutrients through atmospheric deposition, including contributing P (Mahowald et al., 2008), both directly through the deposition of compounds containing PO_4^{3-} that are derived from volcanic aerosols, and indirectly through the addition of various acidic aerosols – which aid dissolution processes – and the P-bearing glass shards or pumice fragments, and apatite crystals. Glass is very rapidly dissolved via hydrolysis because it is thermodynamically unstable and, being fragmental and often vesicular and porous, has a high surface area to volume ratio and hence breaks down very quickly and at rates closely proportional to geometric surface areas (Wolff-Boenisch et al., 2004; Churchman and Lowe, 2012).

High concentrations of P can occur within eruptive plumes (where it is rapidly oxidised including as PO_4^{3-}), which is typically related to the P content of the

parent magma (Bergametti et al., 1984; Mahowald et al., 2008; Roberts et al., 2019). Metal and crystalline salts, along with volcanic aerosol-derived acids, are adsorbed on volcanic particles as the eruption plume cools (Óskarsson, 1980), and high concentrations of phosphoric and other acid aerosols have been found adsorbed onto glass shards (Frogner et al., 2001; Cronin et al., 2003), which are rapidly released upon contact with water. Therefore, either salts or phosphoric acid aerosols generated during an eruption would provide an almost instantaneous input of P into the ecosystem, along with hydronium ions that will enact the dissolution of accompanying glass and mineral particles deposited on the bog surface.

The indirect route for P to enter Moanatuatua bog would have been through the rapid weathering of volcanic glass and apatite crystals, both in situ after deposition on the peat surface, or earlier within the eruptive plume. Within the eruptive plume, strong acids such as hydrofluoric acid can strip bases, such as phosphate, from the glass and apatite particles, sometimes to such an extent that the leachates can become totally neutralised (Dethier et al., 1981). Uranium, copper, and lead are primarily mobilised this way through the chemical 'enleaching' of glass and crystal particles within the eruption column (Smith et al., 1982).

Glass shards from the rhyolitic Ka and Tp tephras, and from the andesitic-dacitic Tf4, Tf5, and Tf6 cryptotephras, at Moanatuatua bog contain small or trace amounts of P (reported as P_2O_5) (Gehrels, 2009) (Table 5.3). As described earlier, volcanic glass can dissolve rapidly within the acidic bog conditions, releasing P (Le Roux et al., 2006). Gehrels (2009) reported heavy pitting of glass shards at Moanatuatua, particularly of the brown, andesitic to dacitic shards (Tf4, Tf 5& Tf 6) which contain higher amounts of P than the colourless rhyolitic shards (Table 5.3).

Although volcanic glass (including pumiceous forms) is overwhelmingly predominant in the five tephras/cryptotephras in Moanatuatua discussed above, these tephra/cryptotephra deposits also contain the phosphate-group mineral, apatite, in small amounts. Both Tp and Ka contain essential or accessory amounts of apatite (Ewart, 1963; Lowe, 1988; Nairn et al., 2004). Further, natural spring waters fed from water passing through multiple Holocene Taupo-volcano-derived tephras are enriched in P (Timperley, 1983). Cronin et al. (2003) reported that

fluorapatite was deposited during the 1995-96 eruptions of Mt Ruapehu, and the same mineral is likely to have accompanied deposition from the Mt Ruapehu-sourced Tufa Trig tephras identified in Moanatuatua bog by Gehrels (2009). The weathering of apatite in volcanic soils is well documented with even the relatively weak carbonic acid produced from microbially respired CO_2 able to mobilise phosphorus from volcanically-derived apatite (Nanzyo, 2002; Dahlgren et al., 2004; McDaniel et al., 2012). The stronger humic acids, which are abundant in peatlands, together with the aerosolic acids deposited concomitantly with glass and crystal particles during an eruption, can also facilitate the dissolution of apatite, making it available for biological uptake (Lobartini et al., 1994); this can happen relatively quickly with the combined presence of apatite and humic acids able to boost plant growth in as little as 30 days (Lobartini et al., 1994). Naturally-occurring apatite was found to completely dissolve within 20 years of deposition in a German raised bog (Le Roux et al., 2006), and biotite was removed rapidly from the Kaharoa Tephra in Kopuatai bog (Hodder et al., 1991).

The mean accumulation rate of P in Moanatuatua of 0.015 g C m^{-2} yr^{-1} is remarkably similar to that of UK peatlands, 0.017 g C m^{-2} yr^{-1} (Schillereff et al., 2016), and for rates measured in peatlands in Ontario, Canada, 0.016 g C m^{-2} yr^{-1} (M. Wang et al., 2015). However, both the C:P and N:P ratios are substantially greater at Moanatuatua than the values reported for the UK and Canadian sites (Wang et al., 2014), indicating that a greater amount of N and C has accumulated relative to P at Moanatuatua. This increase in N and C could be due to the presence of cluster roots in the dominant peat former, *E. robustum*, at Moantuatua, which are known to be highly efficient at recovering P from organic matter via carboxylate extrudation (Lambers et al., 2012, 2013). In Canada, M. Wang et al. (2015) found a strong positive relationship ($R^2 = 0.69$) between C and P accumulation rates, and a similarly strong relationship ($R^2 = 0.76$) between C and N accumulation rates. Here we found even stronger relationships for CAR and P ($R^2 = 0.90$), and for C and N accumulation rates ($R^{2\ =}$ 0.97) (Fig 5.10), suggesting greater control of CAR by nutrient inputs. This close relationship is perhaps to be expected given both the shorter time period investigated and the high variation in nutrient inputs attributed to the five tephra/cryptotephra depositional events. However, the relationship could also be a consequence of the weaker influence of climate on C accumulation in the highly oceanic, mild climate of the North Island of New Zealand. For example, metrics such as photosynthetically active radiation

summed over the growing season, purported to be an important driver of long-term C dynamics in the Northern Hemisphere (Gallego-sala et al., 2018), are less meaningful for the present-day Moanatuatua where growth can occur year-round (Campbell et al., 2014) and photosynthesis can be light-saturated throughout most of the year (Goodrich et al., 2015).

During periods of rapid C accumulation, concentrations of elements taken up by plant growth, but not limiting to plant growth, such as Mg and Ca, become depleted (Figure 7). Although we are more cautious in interpreting the variations in the abundance of these elements through time, changes in their concentration nevertheless are consistent with rapid peat accumulation (M. Wang et al., 2015).

Our study adds to a growing body of literature showing the importance of atmospheric inputs as a driver of C accumulation in ombrotrophic bogs (Glaser et al., 2013; Fiałkiewicz-Kozieł et al., 2016; Kylander et al., 2018). P deposition in the central North Island of New Zealand, 0.040 g C m^{-2} yr^{-1} (Fish, 1976; Tipping et al., 2014), is above the global average, and higher than rates of 0.015 g C m^{-2} yr^{-1} in the far north of New Zealand (Chen et al., 1985). High fertiliser drift due to aerial topdressing has been found to alter the nutrient dynamics and successional ecology of New Zealand forests located less than 30 km from one of our study sites (Stevenson, 2004). New Zealand is also experiencing elevated aeolian dust inputs because of land-use change in Australia (Brahney et al., 2019). These local changes are part of a wider global trend of elevated P deposition (Brahney et al., 2015) with almost half of atmospherically-deposited P estimated to be derived from the burning of fossil fuel (R. Wang et al., 2015), and a significant amount suspected to be from land-use change (Brahney et al., 2015). For example, remote, alpine ecosystems in the western United States have undergone more than a fivefold increase in inputs of K, Mg, Ca, N, and P since the start of the 19th century, which is attributed primarily to increased agricultural activity (Neff et al., 2008). Elsewhere, monitoring sites in Europe, located close to farmland, register rates of P input which are an order of magnitude higher than the global average (Tipping et al., 2014). In other instances, human activities have caused an increase in dust inputs into ecosystems (McConnell et al., 2007; Fiałkiewicz-Kozieł et al., 2016; 2020; Mullan-Boudreau et al., 2017), which implies greater atmospheric deposition of P. Considering the sensitivity of CAR at Moanatuatua bog to periods of enhanced inorganic deposition from tephra (and associated aerosol)

fallout, we suggest that the high rate of CO_2 uptake in the present day (e.g. 69 g C cm^{-2} yr^{-1} for Moanatuatua and 2013 g C cm^{-2} yr^{-1} for Kopuatai as reported in Ratcliffe et al., 2019a) could be due to increased P inputs, potentially from local and distant sources, but this hypothesis would need to be verified through monitoring of present-day P deposition.

5.8 Conclusions

In the context of 21st-century changes to global nutrient cycling, it is important to understand how peatlands have responded to nutrient inputs in the past. We measured elemental accumulation across a c. 1000 year period in a northern New Zealand bog spanning two large volcanic depositional events and three smaller events. Volcanoes can deliver phosphorus to ecosystems through a variety of mechanisms, and the presence of the phosphate-rich mineral apatite and the presence of phosphorus within easily-weatherable volcanic glass support the contention that volcanic eruptions have been a source of elevated phosphorus inputs into Moanatuatua bog.

We found peatland carbon accumulation to be highly coupled to nitrogen and phosphorus accumulation, with quite consistent stoichiometric ratios being maintained, allowing carbon accumulation to increase rapidly following ash deposition from eruptive events. Deposition of volcanic material coincided with small shifts in stoichiometric ratios, indicating a greater abundance of phosphorus during these times. Such events coincided with increases in the concentration of trace metals of volcanic origin with a high affinity for organic matter such as lead, uranium, and copper, providing evidence for acidic leaching of elements from volcanic glass, either within the eruption plume or following deposition in the peatland, or both.

We conclude that long-term carbon accumulation rates in New Zealand bogs were, and likely still are, primarily constrained by nutrients rather than direct climatic drivers such as temperature or moisture availability. Similar findings, pointing to the pivotal role of phosphorus in peatland C cycling in Japanese and Swedish bogs, suggests this phenomenon is not limited to New Zealand. It is notable that, despite a large number of investigations, peatland long-term carbon accumulation has only been found to have a relatively weak correlation with climatic variables (e.g. the strongest climatic correlation found by Gallego-sala et al., 2018 was an

R^2 of 0.2 for photosynthetically active radiation summed over the growing season). This is in stark contrast with the results presented here, and in a small number of other studies, which have also considered past nutrient inputs. Our results, and those of the aforementioned studies, show that nutrients, phosphorus in particular, exert a strong influence on long-term peatland carbon dynamics. Phosphorus inputs, at least in some peatlands, may exert a greater influence on peatland carbon accumulation than direct climatic forcing.

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Chapter Six

Discussion and Conclusions

6.1 Overview of the main topics and objectives of this thesis

This thesis is primarily concerned with the drivers of carbon accumulation, over different timescales, with an emphasis on the effects of drying. While the focus of the thesis was initially solely on the water table as a driver of CO_2 dynamics, the role of nutrients became an increasingly important consideration. This was due to a strong association found between C accumulation rates and volcanic eruptive events within the long-term peat record (Chapter 5). Thus, nutrients are discussed as an important driver of long-term C dynamics in the third results chapter.

6.2 Overview of Chapter 3

The first thesis objective addressed in Chapter 3 published as Ratcliffe et al. (2019) was to compare CO_2 fluxes in a near pristine bog (Kopuatai) with a drainage-affected bog (Moanatuatua), both restiad bogs. This investigation found both sites to be contemporary sinks for CO_2 but also determined a number of important differences in the two ecosystems. Component CO_2 fluxes, which result from processes which cause ecosystems to lose CO_2 (ER) and take up CO_2 (GPP), were much greater in magnitude at Moanatuatua. Carbon uptake at Moanatuatua had greater seasonal variation than at Kopuatai, with the largest difference in GPP between the sites occurring during the summer months. Greater ER and GPP at Moanatuatua indicated a faster turnover of carbon, greater CO_2 uptake by the ecosystem, manifested through greater annual GPP and the light response of the plants, was able to partially compensate for higher respiration with the result that Moanatuatua remained a carbon sink but was overall a weaker CO_2 sink than was found for Kopuatai.

There were important differences in how the two sites responded to low water tables. For both sites, dry conditions could reduce net CO_2 uptake but this occurred through opposing mechanisms. At Kopuatai, low water tables promoted increased ER, also found by Goodrich et al. (2017), while at Moanatuatua there was no evidence of this and ER appeared to be driven more by temperature as has been found for dry bogs elsewhere (e.g. Lafleur et al., 2005). Conversely, plant

community uptake of CO_2 via GPP was restricted at Moanatuatua under water table extremes, but this did not occur at Kopuatai. We drew upon the literature for mechanistic explanations to explain the differences we observed in GPP and ER. It is not unusual for dry bogs to have no response of ecosystem respiration to water table movement (Table 2.2). This is thought to occur when the range of water table fluctuation is incapable of promoting biologically meaningful changes in peat moisture content, in zones where the chemical and physical composition of the peat would normally permit a relatively high level of microbial activity, especially near the surface, where the majority of heterotrophic respiration occurs, and also the deeper peat which has not been exposed to oxidising conditions for a period of decades or more (Lafleur et al., 2005). At Koputai bog, where the hydrology is largely intact, the moisture content in the surface peat is usually high enough to restrict heterotrophic respiration but can drop to a level which removes this restriction in late summer and at times of drought (Goodrich et al., 2017) in agreement with more pristine sites (Chapter Two, Table 2.2).

Differences in the plant community between the two sites, predominantly the shrub *Epacris pauciflora*, was surmised to be the most likely explanation for the different response of GPP to water table in the two bogs. Ericoid shrubs, unlike other major components of the bog's plant community, cannot tolerate water-logging in the rooting zone (Shaw et al., 1990; Read, 1996) and as such ericoids are physiologically poorly equipped for fluctuating water tables. Ericoids, such as *E. pauciflora* likely face a difficult physiological compromise when growing in conditions as found at Moanatuatua. Water-logging and thus root mortality can occur in the winter, however, roots which avoid water-logging in winter may suffer from desiccation in the summer (Read, 1996). Ericoids typically decline in abundance with increasing water table fluctuation (Rutter, 1955). Restiad species, in contrast, and somewhat paradoxically, have evolved in arid environments and have maintained many of the functional adaptions to surviving desiccation (Linder and Rudall, 2005). The wetland restiads of Australia, for example, are not described as primarily wetland species; instead, they are adapted to nutrient-scarce environments with seasonal inundation and desiccation (Pate and Meney, 1999; Linder and Rudall, 2005). The main peat former at Moanatuatua and Kopuatai *Empodisma robustum*, has a deep taproot (Clarkson et al., 2009), equipped with aerenchyma which allows survival in anoxic conditions (Campbell, 1964), and should permit access to water even when the water table is very low.

6.3 Overview of Chapter Four

The second thesis objective was to re-visit Moanatuatua bog after a 16-year interval and conduct new measurements of CO_2 exchange. The results of this investigation are presented in Chapter Four. This work was complimentary to the inter-site comparison between Kopuatai and Moanatuatua, this time looking at how the dry bog had changed with time rather than how it differed to a near-pristine site. Re-analysis of old data from 1999 and 2000 (Campbell et al., 2014) revealed quite a different situation to what was previously understood for Moanatuatua in those earlier years post-drainage. Rather than the strong sink for CO_2 reported, the site was found to be a moderate-to-large source for CO_2. This discrepancy was found to be predominantly due to the water vapour dilution correction being incorrectly applied to the original data, but considerable differences also occurred as a result of implementing quality control flags, standardised statistical tests and an updated spectral correction procedure (Chapter Four, this thesis). This brings Moanatuatua more into line with what would be expected following a dramatic lowering of the water table (Laiho, 2006), such as that which occurred between 1979 and 1994 (Chapter Four, this thesis). Fundamental ecosystem properties, inferred from light response parameters, demonstrated the earlier period at Moanatuatua to have had lower photosynthetic capacity across all seasons and to be less seasonally variable that it is now. Seasonality, in the earlier period, was more comparable with modern day Kopuatai than modern day Moanatuatua, while photosynthetic capacity was found to sit almost equidistant between Kopuatai and modern Moanatuatua. Another important trend in the flux data for modern Moanatuatua was a reduction in ecosystem respiration. This was apparent despite greater photosynthesis and warmer air temperatures, both of which would normally be expected to result in higher ecosystem respiration, all other factors being the same (Lloyd & Taylor, 1994; Baldocchi and Penuelas, 2019). The most likely explanation for this, although it requires further confirmation, is a decline in organic matter quality which would be expected after prolonged exposure of the peat to oxic decay (Leifeld et al., 2012; Könönen et al., 2016). However, a number of other factors could be responsible for such a decline, not least the expansion of shrub cover which can reduce heterotrophic respiration through shading (Frost et al., 2018), and through an as yet unproven mechanism, suspected to be based on plants outcompeting microbes for nutrients, resulting in changes to microbial ecology

(Ward et al., 2009, 2015). When CO_2 flux measurements were first carried out, in 1999 and 2000 (Smith, 2003; Campbell et al., 2014), the shrub *E. pauciflora* was just starting to respond to the drier conditions and was described as a minor, albeit rapidly expanding part of the plant community (Smith, 2003). In summary we concluded it was likely that the greater prevalence of *E. pauciflora* contributed to the greater GPP in the present day, and may have a possible role in the decline in ER. Both of these statements require further investigation, which would be best conducted at the plot, or plant scale.

6.4 Overview of Chapter Five

The third thesis objective was to investigate the drivers of peatland carbon accumulation rate at the 50-100 year timescale, measuring C accumulation in unprecedented temporal detail for New Zealand bogs, and at a resolution which is rare in an international context (Mauquoy et al., 2002). The time period investigated (~1200 years) was also intended to be long enough to detect other intermittent disturbances, with information available in theses and literature for changes local in climate (Hazell, 2004; Lorrey et al., 2008; Jara et al., 2017), plant species (Hazell, 2004; Haenfling et al., 2017; Jara et al., 2017), tephra deposition (Gehrels, 2009), and fire frequency (Jara et al., 2017) available for the site and a greater number of other records, for paleoclimate and environmental change for other sites close by (e.g. Newnham and Green, 1989). However, upon examination of the long-term C accumulation data, it became apparent that the record was dominated by two periods of rapid C accumulation, concurrent with two large eruptive events preserved as ryolitic tephra layers contained within the peat. In addition, further consultation of the eruptive record and stratigraphic position of tephra layers at Moanatuatua (Gehrels, 2009) indicated a number of smaller changes in C accumulation rate occurred at depths consistent with the presence of smaller, but more nutrient rich, andesitic Tufa Trig eruptions, which are poorly dated (Donoghue et al., 1997). As such, we considered it very difficult to separate out any record of climate forcing considering the strong role volcanism seems to play in the long-term carbon accumulation dynamics and the high number of eruptive events present in the chronological sequence we have obtained. This finding is in itself of great interest in terms of carbon cycling, not least because the changes in carbon accumulation rate are large (4-5 times the background rate) and as close to instantaneous as can reasonably be inferred in a

palaeoecological context. Importantly, C accumulation rate accelerated from a background rate which is 'typical' of long-term carbon accumulation (Schipper and Mcleod, 2002; Yu et al., 2010) to one which is much closer to the modern day value measured at Kopuatai bog (Goodrich et al., 2017) and inferred from CO_2 uptake in (Ratcliffe et al., 2019) as well as in a number of other sites globally (Ratcliffe et al., 2018). Tephra deposition events were synchronous with a shift towards greater phosphorus in the C:P and N:P stoichiometric ratios, i.e. lower ratios, suggesting a nutrient driven mechanism. This is consistent with one other example from the literature where Hughes et al (2013) found volcanic inputs to increase carbon accumulation rate due to phosphorus inputs.

Our findings add to a small, but growing, pool of literature which shows past carbon uptake in peatlands to be highly sensitive to inputs of phosphorus (Hughes et al., 2013; Kylander et al., 2018) or, when phosphorus is not measured, inorganic matter generally (Fiałkiewicz-Kozieł et al., 2016) and considerable anecdotal evidence that indicates high carbon accumulation rates are possible in some peatlands with high nutrient loading (Payne et al., 2019). Such findings are consistent with some contemporary fertilisation studies in bogs (Aerts et al., 1992; Lund et al., 2009) which result in increased plant productivity. Importantly, palaeoecological studies can provide insight into a time when there had been little alteration of the global phosphorus cycle, whereas modern-day fertilisation studies are almost certainly taking place against a background of elevated P deposition and as such lack a suitable control. We hypothesise that the high rates of CO_2 uptake in the present day at Moanatuatua and Kopuatai are likely to be due to elevated nutrient inputs, due to human activity both locally (Stevenson, 2004; Tipping et al., 2014) and potentially remotely due to land use change in Australia (Brahney et al., 2019). The results of Chapter 5 suggest nutrient-related controls on C cycling are highly important in restiad peatlands, as appears to be the case for *Sphagnum* peatlands also (Hughes et al., 2013; Kylander et al., 2018). We conclude that studies of peatland carbon cycling, regardless of timescale, should consider mineral inputs, along with climate, as a driver of peatland C accumulation, with the additional consideration that climate changes and nutrient cycling will be to an extent coupled. For instance changes in humidity and airflow patterns are also known to influence nutrient inputs (Glaser et al., 2013; Kylander et al., 2018).

6.5 Broader implications of the findings of this thesis

The work embodied in this thesis highlights the adaptability of the restiad peatland plant community and how this can prevent large CO_2 losses even in the face of large changes in the water table. In Chapter 2, the thesis literature review, the importance of theoretical frameworks was emphasised. For instance, the wide array of responses to water table recorded in the contemporary flux literature only appears (relatively) consistent when the baseline hydrological state of the ecosystem is considered (Chapter 2, this thesis) as theorised by Belyea and Clymo (2001). The results of Chapters Three and Four show that Moanatuatua and Kopuatai fit into this framework, with Kopuatai responding in a way which is consistent with wet bogs and Moanatuatua responding as a dry bog may be expected to. These results serve to stress the importance of the peatland plant community as a driver of CO_2 fluxes. To use an analogy, the plant community is the 'lens', or the intermediary through which external drivers will primarily affect carbon fluxes in peatlands. The restiad plant community has shown itself to be exceedingly resilient to external perturbations, particularly drying, as was also found by Goodrich et al. (2017), and this has resulted in a stability of the carbon sink which is unusual in an international context, for instance, compared to a *Sphagnum* moss dominated communities (Laitinen et al., 2008). The resilience of the restiad plant community is not surprising when both the evolutionary history of restiads and their unusual physiology (from a peat-forming perspective) is considered (Linder and Rudall, 2005; Wagstaff and Clarkson, 2012; West et al., 2012). Despite the extraordinary resilience of the restiad plant community, there have been important changes at the species level, and these could have important consequences for carbon storage in the future. Chief among these changes is the expansion of the ericaceous shrub *E. pauciflora*. The long-term consequences of this for nutrient cycling and the local water balance require further investigation. The work carried out in Chapter Three suggests an optimal water table depth of between 400 mm and 700 mm is optimal for CO_2 uptake at Moanatuatua (Ratcliffe et al., 2019), which is exceedingly deep in an international context. For instance 150 mm was found to be optimal by Belyea and Clymo (2001). What may be more important to consider in the long-run is the rate of material transfer into the anaerobic catotelm (Tolonen and Turunen, 1996), which is likely to be negligible given that 700 mm depth represents peat between 700 and 1000 years old (Gehrels, 2009; Jara et al., 2017).

6.5.1 Considering the stability of the peatland carbon sink

We have inferred that the resilience of the carbon sink at Moanatuatua is due primarily to the unusual traits of the restiad plant community. These findings are also applicable to other peat types if viewed using the concept of plant functional traits (Lavorel and Garnier, 2002). Key factors which have allowed the carbon sink to persist are:

- Tolerance of a fluctuating water table and the ability to increase CO_2 uptake through primary productivity in response to drying (which may be linked to nutrient inputs).
- Chemical resistance of litter to decay, which appears to have increased recently after drying.

As such, we anticipate that peatlands elsewhere which are able to tolerate a fluctuating water table, without loss of the peat-forming community, are likely to be more resilient to drying. Restiad peatlands may be analogous to the pocosin shrub-formed peatlands of the Atlantic coast of the USA (H. Wang et al., 2015), where the peatland CO_2 uptake can remain resilient despite low summer water tables, with the dominant peat former being both tolerant to drying and capable of forming litter highly resistant to decay, for example with a high level of phenolics (H. Wang et al., 2015). Vascular peatland species, common in the Northern Hemisphere, such as *Eriophorum spp*. and *Molinia caerulea* are similarly well adapted to fluctuating water tables (Taylor et al., 2001) and while relatively poor peat-formers, their resilience to drying might prevent large losses of C (Gogo et al., 2011; Gatis et al., 2016).

6.5.2 Considering shrub expansion locally and globally

The expansion of ericoid shrubs onto a drying Moanatuatua is a phenomenon that is documented in other restiad peatlands (Newnham et al., 2012) and one that is shared with Northern Hemisphere peatlands, where shrubs are rapidly colonising vast areas of natural peatland (Berg et al., 2009; McPartland et al., 2018), impacted peatlands (Stewart and Lance, 1991), and the poorly classified organic soils in the tundra at high latitudes (Wrona et al., 2016). The net effect of shrubs on peatland C balance is highly uncertain, and there is debate across a range of topics, including the long-term stability of the shrub community (Holmgren et al., 2015; Wang et al., 2017). The nutrient acquisition strategy of ericoids is

concerning from a carbon perspective, as they are known to microbially prime peat in order to break down the organic complexes within the peat and scavenge nutrients such as nitrogen and phosphorus which are required for growth (Read, 1996; Walker et al., 2016; Wang et al., 2017) and ericoids can promote loss of so called 'ancient' carbon (Walker et al., 2016) which would otherwise remain relatively stable. In contrast, 'peat-formers' such as *Sphagnum* and *Empodisma* use their high cation exchange capacity (Puustjärvi, 1959; Agnew et al., 1993; van Breemen, 1995), combined with other physiological adaptations, to scavenge nutrients from rainwater and atmospheric fallout before other plants can access these (van Breemen, 1995; Clarkson et al., 2009; Wagstaff and Clarkson, 2012). However, it has also been found that ericoid shrubs increase the chemical resistance of the peat to microbial decay by selectively removing nutrients, in preference to carbon, thus placing stoichiometric constraints on further mineralisation (Ward et al., 2009) and the net effect on CO_2 flux is uncertain and requires further study. Any change in ER must also be weighed against the greater productivity often found in ericoid shrubs in comparison to other peatland species (Bubier et al., 2003; Peichl et al., 2018) which is supported by our ecosystem scale GPP measurements (Chapters Three and Four).

Our results are consistent with the theory of ericoid shrubs having a stabilising effect on the carbon balance as proposed by H. Wang et al. (2015), with the data from Chapters Three and Four highly suggestive of *E. pauciflora* being responsible for higher CO_2 uptake, however, it is very difficult to make any inferences on the effect of *E. pauciflora* on ER. Ecosystem respiration has declined over the same period when *E. pauciflora* has expanded, but other explanations, for instance declining organic matter quality, offer a simpler explanation for this. Importantly, the higher uptake of CO_2 at Moanatuatua is essential if the site is to remain a CO_2 sink, and as such *E. pauciflora* could be playing an important role in maintaining CO_2 sink function. However, the long term effects of continued *E. pauciflora* dominance are uncertain. Evaporative drying and long-term changes in peat water storage capacity remain a threat to the ecosystem C store in the future.

6.5.3 The role of nutrients in peatland carbon cycling

While the restiad plant community at Moanatuatua, and through it the CO_2 sink, has been relatively resilient to water table drawdown, the results of Chapter Five

indicate the ecosystem may be highly sensitive to inputs of nutrients such as phosphorus. Until recently it was thought that human alteration of the atmospheric component of the phosphorus cycle was minor (~5% of total deposition in Mahowald et al., 2008). However, recent studies estimate the true figure to be as much higher, for instance, 50% in R. Wang et al. (2015). Additionally, changes to global phosphorus cycling are likely to be high enough to have impacted nutrient cycling in remote alpine ecosystems (Neff et al., 2008; Brahney et al., 2015). Sites adjacent to pastoral lands, such as Moanatuatua, can be expected to have deposition rates an order of magnitude greater than others (Tipping et al., 2014) and land clearance can cause lasting impacts to peatland ecology through dust inputs (Ireland and Booth, 2012), this is consistent with a trend of increasing N and P (Chapter Four). Atmospheric phosphorus has received surprisingly little attention as a driver of peatland carbon cycling, but the work we present here and a handful of other recent studies, suggest the impact of changes in phosphorus inputs could be an important driver of peatland carbon and peatland ecology generally. The effects of phosphorus inputs appear to be rapid and elicit a strong response in peatland carbon cycling, but there are too few examples in the literature to make broad generalisations as yet concerning the role phosphorus may play globally in peatland C dynamics. However, it should be noted that researchers concerned with phosphate cycling have singled out ombrotrophic bogs as one of the ecosystems most likely to be affected by phosphorus deposition (Tipping et al., 2014). We promulgate that given what limited information we have on the effects of phosphorus in peatlands, presented in this thesis and elsewhere, considerably more research attention is warranted. Furthermore, an important consideration for future studies, and especially for researchers looking at fertilisation studies, is that contemporary peatlands, even those located in remote locations, are quite possibly already subject to an elevated level of phosphorus inputs compared to times in the past. Therefore, future studies looking at the effect of increased nutrient inputs should measure phosphorus deposition and take this into consideration.

While we have not speculated as to the plant community response to nutrient inputs, woody layers above the Taupo tephra would suggest that shrub growth could be implicated in the higher C accumulation, as it appears to be at Moanatuatua in the present day. It should be noted, however, that very high rates

of contemporary C accumulation rates can be sustained by a almost pure *E. robustum* community, with little to no shrubs.

6.5.4 In summary

We found the CO_2 sink to be resilient to long-term hydrological change at Moanatuata, even though dry conditions were capable of reducing it. The level of resilience at Moanatuatua is unusual in an international context but makes sense when the evolutionary history of the main peat former, *E. robustum*, is considered. The CO_2 sink is resistant to drying, over the timescale of ~20-40 years, for a number of reasons, most importantly the increased uptake of CO_2 from the plant community, which we believe to be due to the increased presence of ericoid shrubs. A long term decline in ecosystem respiration is another important mechanism which we hypothesise is due to declining organic matter quality, but this remains something to be explored. It should be noted that while low water tables at Moanatuatua and Kopuatai are capable of decreasing the carbon sink strength, the decline is still minor and both sites are still capable of sequestering carbon (implied from CO_2 exchange, and in addition measured for Kopuatai by Goodrich et al., 2017) at a rate greater than typical long-term values. When long-term carbon accumulation rate was investigated, we found there had been a rapid increase in C accumulation, which elevated C accumulation from a rate typical of long-term background C accumulation to a rate comparable to the modern CO_2 uptake, as such we conclude that while the peatland ecosystem is highly resilient to drying, nutrient inputs in the present day are likely to be exerting a strong influence on the ecosystem.

6.6 Recommendations for Further Research

6.6.1 CO_2 fluxes, peatland ecology and the influence of nutrients

In order to make study findings applicable to a wide range of peatlands, there is a clear need for the peatland flux community to move beyond producing an ever greater number of records of annual carbon balance and to emphasize consideration of the mechanisms and processes which are driving CO_2 fluxes and why specifically each site is responding in the way it does. This will require closer collaboration with ecologists, geochemists, hydrologists, plant physiologists and palaeoecologists. It will also require greater consideration of peatland theory and theoretical models (e.g. Belyea et al., 2009; Hilbert 2000). In light of the findings

of this thesis, we highlight the effects of nutrients and the plant level response as areas which particularly warrant further attention.

- The natural continuation of this thesis would be to look at present-day nutrient inputs in peatlands, to determine whether they are elevated at sites with high CO_2 uptake (such as Moanatuatua and Kopuatai) compared to others where NEP is consistently lower.
- Isotopes of oxygen bound to phosphorus can be used to provenance contemporary phosphorus inputs, distinguishing between volcanic, erosive and fertiliser sources (Tamburini et al., 2013), this would clearly be useful for studying contemporary impacts of phosphorus deposition on carbon cycling and, with some method development, might have potential for studying the impact of volcanism vs. terrestrial dust as a driver of C accumulation in the past.
- Species-level measurements of photosynthesis and plant 'stress' and how this differs both seasonally and with water table depth are required to further test some of the mechanisms behind the ecosystem CO_2 flux changes found in this thesis.
- It would be useful to know the maximum theoretical carbon uptake of different peatland plants, if climatic and nutrient-related restrictions are removed, There is further need to understand both the absolute and the competitive optima for climate and nutrient loading for a wide range of peatland plants. This is probably best achieved using greenhouses where the climate, light and nutrient inputs can be tightly controlled.
- The different nutrient acquisition strategies of peatland plants could lead to interesting ecological interactions and effects from nutrient deposition as also hypothesised in Clarkson et al. (2009). For instance, it is conceivable that extreme scarcity of nutrients could favour plants which acquire nutrients from the mineralisation of peat, rather than those which rely primarily on atmospheric inputs. If this is the case, then there could be important implications for contemporary peatland ecology and the interpretations made from the paleoclimate record.
- The importance of nutrient inputs for carbon accumulation at our site and elsewhere raises concerns about studies only considering climatic factors

as a driver of carbon accumulation. Nutrient inputs will be closely coupled to atmospheric circulation, due to a high proportion of mineral inputs for New Zealand, and elsewhere, coming from distant arid landscapes such as the Sahara desert and Australia (Marx et al., 2009; Glaser et al., 2013). Changes in C dynamics which have been assumed to have been directly caused by climate, could be in part due to indirect changes in nutrient inputs.

- Is restiad peat fundamentally more resistant to oxidative decay than other peat types? Our results in Chapter 5 suggest a higher portion of phosphorus is recovered from the peat than is the case for sphagnum peatlands, consistent with what is known about the ability of cluster roots to recover phosphorus. Additionally, there may be compounds within the peat, such as high levels of phenolics found in pocosin peatlands, which may restrict microbial decay, very little is known about the organic chemistry of restiad peat.

6.6.2 Thresholds of resilience to change

There is still a high degree of uncertainty as to the climatic envelope within which peat can form. If this is to be addressed then peatlands on the bioclimatic fringe, and particularly relic peatlands, warrant further attention. New Zealand peatlands are interesting as human influence can be excluded up until the last ~800 years and opposing tends in Southern Hemisphere insolation allow the testing of drivers of long-term carbon accumulation rates developed for the Northern Hemisphere (e.g. Yu et al., 2010; Charman et al., 2015). From a carbon cycling perspective, there is an urgent need to determine the threshold of nutrient loading, before a loss of function, for peatlands both locally in New Zealand and globally. For Moanatuatua, N and P appear to be accumulating in the surface peat, suggesting that the ecosystem's capacity to utilise these nutrients has been overwhelmed. This could have important consequences for the continued resilience of the ecosystem. It is highly likely that there will be interacting effects with climate, for instance with climatic perturbations limiting the ability of the peat-formers to lock nutrients away in organic matter, which is a known strategy Sphagnum (van Breemen, 1995) and *Empodisma* (Clarkson et al., 2009) employ to limit competition.

- What are the thresholds of nutrient loading above which nutrients can become enriched within the surface layers, at what point does this permit the invasion of peatlands by non-peat-forming species?

6.6.3 Important considerations for palaeoscience

Plaeoecologists often assume climate, and increasingly disturbance and internal feedbacks as drivers of change. Our findings and others such as Glaser et al., (2013) and Kylander et al., (2018) indicate the role of nutrients has been underestimated. Stoichiometry, trace element geochemistry and mineralogy could be used in future studies to better assess the role changing nutrients may play.

- Recommend that mineral inputs, particularly those associated with phosphorus are considered when paleoclimatic inferences are made from peat records.
- The chronology of palaeoecological records from peatlands affected by volcanism are likely more variable than previously thought, and there could be considerable errors, aka. loss of high frequency variability, in the chronologies following eruptions.This is likely if records are dated at low resolution, or rely on tephra layers as a substitute for radiocarbon.

6.7 What can New Zealand peatlands contribute to global understanding?

Peatlands in New Zealand are uniquely positioned to answer many difficult questions faced by the research community. From an evolutionary perspective, they are fascinating, becoming the functional analogue of *Sphagnum* peatlands, despite a very different developmental pathway. The broad range of conditions *Empodisma robustum* can tolerate (Hodges and Rapson, 2010) is in contrast to the high degree of specialisation found in individual sphagnum species (Gunnarsson et al., 2011). This should make assessing the functional limits of the peatland easier. Despite being older than the majority of other temperate peatlands restiad peatlands offer a paleoecological record which spans glacial cycles, also spanning greater climate variability than other temperate bogs, once again making it easier to understand the bioclimatic thresholds which influence the carbon sink.

6.8 Concluding Remarks

The investigations presented in this thesis indicate a surprising resilience of the restiad peatland C sink in the face of extreme drying. This was due primarily to the ability of the restiad plant community to increase primary production under drier conditions. The ability to increase primary production is in turn linked to the specific adaptations and morphology of the restiad peat formers but is also more generally permitted due to a lack of strong climatic and nutritional constraints on present-day growth in these ecosystems. The palaeoecological investigations presented in Chapter 5 reveal C accumulation to have been highly coupled with nutrient availability, and nutritional restrictions to growth are likely to be weaker now than in the past due to the land-use changes in the neighbouring landscape. However, if nutritional, climatic and hydraulical constraints to growth are weak, or perhaps even nonexistent, will *Empodisma robustum* continue to out-compete non-peatformers going into the future? In order to understand the stability of these ecosystems much more needs to be understood about the specific hydrological-climate-nutritional niche of *E robustom* and how it compares with other peat-formers and peat-forming communities.

The role of plant productivity in maintaining the ecosystem carbon sink was clear from the results of this thesis. In contrast, the role the peat litter itself is more obscure. Declining ecosystem respiration, strongly suspected to be driven by a decline in organic matter quality and heterotrophic respiration, has contributed to the resilience of our dry site. But it is not known whether this peat differs substantially from that of other peatlands, for instance, if restiad peat has greater chemical resistance to decay, or if the apparent depletion of phosphorus in the peat, relative to Northern Hemisphere reference sites in the literature, imposes stoichiometric constraints on decay.

New Zealand peatlands have much to contribute to the global understanding of how peatland ecosystems work. Peat formation is not merely an accident of nature, but a clear competitive strategy, employed by a diverse range of plants with highly differing taxonomic backgrounds, across wide geographical areas. Peat formation has developed to give slow-growing nutrient conservative plants a competitive advantage over faster-growing more nutrient demanding competitors and peatland formation and stability have been honed following evolutionary principles. These in turn lead to the complex array of processes and feedbacks

which maintain ecosystem stability over time and many of these we are just starting to understand. Northern Hemisphere peatlands typically have a much greater number of peat-forming plant species, each with its narrow ecohydrological niche. The complexity of northern and tropical peatland plant communities is not replicated in restiad peatlands. Here we have something akin to a 'Darwinian Demon' of peat formation, while admittedly slow to reproduce and grow, unlike the classic Darwinian Demon, the analogy applies to the wide range of conditions *E. robustum* can successfully outcompete other plants. *E. robustum* is seemingly tolerant and well adapted to a range of conditions, yet, for the time being, still able to out-compete non-peatland species even in a highly impacted ecosystem such as Moanatuatua. The dominance *of E robustim* greatly simplifies one of the most complex aspects of peatland ecology, the rapid species turnover that usually occurs in other peatlands undergoing change. As such, restiad peatlands offer an ideal testing ground for theories and models of peatland ecosystem function. Restiad peatlands are only just starting to be understood, and still have a great deal to contribute to global understanding of peatland ecosystems.

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Supplementary Table 1. Research carried out at Moanatuatua, with the date if known. Presented along with a brief summary of what was recorded and anything exceptional or what might be of general interest. Note, the name Moanatuatua has only been in consistent use in the literature since about 1960. Moana-vale and Roto-o-rangi are also used prior to 1960.

Observations or research carried out	**Date**	**Reference**	**Comments**
Observations of Sporadanthus, misidentified as *Sporadanthus traversii*	1879	Cheeseman (1879)	
Observations on the central drain parallel to Wallace road	1893	Cussen (1893)	Mentions the central drain from the bog has eroded 70ft into alluvial sediment
Mentions land conversion practices at the time	1917	Reynolds (1917)	Theorised that the peat was formed by Maori eel-weirs (and that there was good soil under it)
Total moisture, loss on ignition, nutrient content.	1917	Aston (1917)	From Trecarne, otherwise known as Monavale? Eastern Moanatuatua as it was in the process of 'breaking in' Land owner at the time favoured very deep drainage and regular burning.
Depth survey	1930s	Grange et al. (1939)	Does not include present day reserve.
Surface contours	1930s	Grange et al.,(1939)	Peat dome 15 meters above surrounding land
Vegetation survey & Ecological description	1930s	Cranwell (1939)	
Brief vegetation description	1952	Osvald (1952)	First call for protection of peatlands in New Zealand
Geochemistry of the organic faction of Moa and Hauraki	1952	Bailey (1953)	
Vegetation survey & plant macrofossils, pollen	1953	Cranwell (1953)	Core taken from the Manuka zone at the edge of the bog.
Protozoa in diversity in centre and margins of the bog	1958	Stroud (1958)	
Bacteriology of the peat	1958	Stout (1958)	
Vegetation survey	1964	Campbell (1964)	Bog had been recently burnt, likely Bev has some photos from this visit

Observations or research carried out	Date	Reference	Comments
Vegetation survey, Soil pH, nutrient content	1965	Butcher (1965)	Also speaks about recent burning. Data is all really vague stuff from Hupkens van der Elst
PhD study	1961-1964	Armishaw (1964)	Copies available from the University of Waikato library
Etymology, water table, some information about the vegetation, nutrient content	1967-1968	Luxton (1982)	Very useful document with reliable data. Somewhat obscure topic, mentions surface moisture, part of a series.
General vegetation, water table description	1969	Purdie (1969)	
General description		Campbell (1971)	"the vegetation of Waikato bogs"
Rotifers at Moanatuatua		Haigh (1971)	
General vegetation description		Bates (1973)	
Undergraduate project, pH, Water table, Vegetation survey, vegetation height.	1974	Dickinson (1974)	This is Bev Clarkson, Dickinson is her maiden name
Depth survey	1977	Davoren (1978)	Includes a few points within the reserve
Undergraduate project	1978	Groote 1978	Never been able to locate
MSc study, regeneration post fire, vegetation survey, peat water content, pH, ash content, humification, surface contours, water table depth, evapo-transpiration, soil temperature.	1978-1979	Matheson (1979)	Useful document, one of the earliest with reliable data
Enzyme activity, pH, C and N content data	1981	Sarathchandra et al. (1981)	
Series of radiocarbon dates	1982	(Hogg et al., 1987)	Likely this area has been converted to pasture, little to no supporting information.

Observations or research carried out	Date	Reference	Comments
Nutrients, pH, C, N content, C/N ratios from converted peatland at Moanatuatua	1987	Perrott and Sarathchandra (1989)	
Pollen record	1989	Newnham et al. (1989)	From lake near Moanatuatua
Potassium measurements from peat	1990	Williams et al. (1990)	
Empodisma photosynthesis and water loss, water table depth	1995	Sharp (1995)	
Post fire recovery, vegetation survey	1984-1997	Clarkson (1997)	
Stratigraphy, crude humification	1997	Shearer (1997)	
Vegetation Biomass and density, leaf area index, nitrogen content, water use efficiency, peat moisture content, bulk density, conductivity, pH, nutrient content, water table, energy balance and evaporation.	1995-1996	Thompson (1997)	
Peat geochemistry, fungal analysis	1998	Kuder (1998)	Comparison with Kopuatai, chronology out.
Sporodanthus taxonomy	1999	De lange et al. (1999)	
Carbon content in reserve and converted land	2002	Schipper et al. (2002)	Using Taupo tephra
PhD, The Ecology of *Sporodanthus*, the effects of nutrients and water table on *Sporodanthus*. *Sporodanthus* growth	1999	Kelleher (1999)	Comparing growth at Moa and Kop

Observations or research carried out	Date	Reference	Comments
MSc hydraulic flow, water balance, bulk density, humification, hydraulic conductivity, linkage with groundwater system, ground penetrating radar survey, precipitation and evaporation	1999	Grimshaw (2000)	
PhD, Bulk density, partial density, humification, moisture content, loss on ignition, pH, total nitrogen, water table measurements, hydraulic head, peat respiration rates, effects of water table and temperature on respiration.		Hodge (2002)	
Eddy Covariance CO_2 flux, chamber flux measurements, ground heat flux	1998-2000	Smith (2003)	
Bulk density, particle density, organic content, mineral content		Campbell et al. (2002)	Also more information available Laybourne thesis
Relationship between peat and coal deposits…!		Moore and Shearer (2003)	
Subsidence in surrounding agricultural land		Mckenzie and Mcleod (2002)	
Vegetation, Humification (Von Post), pH, Bulk density, LOI, Nutrients NPK		Clarkson et al. (2004)	
Discovery of two Dionella species *Hemerocallidaceae*		Heenan & de Lange (2002)	
Tephrachronology, Radiocarbon dating, peat humification, carbon content, macrofossils, charcoal, testate ameabae, moisture content, water table, pH, conductivity		Hazell (2004)	
Tephrachronology, radiocarbon dates, LOI		Gehrels(2009)	
Subsidence rates in agricultural land near Moanatuatua		Pronger et al. (2014)	

Observations or research carried out	**Date**	**Reference**	**Comments**
Eddy Covariance CO_2 flux	1998-2000	Campbell et al.(2014)	Same data as Smith 2003
δ 13C in *empodisma* and growing conditions		Amesbury et al. (2015)	
Corse macrofossil re-construction of the bogs history		Haenfling et al. (2015)	
Pollen record of the bogs history		Jara et al. (2017)	
Water table and water balance for the site	2015-2018	Dawes (2018)	
Comparison of CO2 exchange at water table with Moanatuatua bog	2015-2017	Ratcliffe et al. (2019)	

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